DOCTOR OF PHILOSOPHY

Ecophysiology of strains A and C of Potamophyrgus jenkinsi

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ECOPHYSIOLOGY OF STRAINS A AND C OF *POTAMOPYRGUS JENKINSI*

A thesis
submitted to the University of Wales

by

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SUMMARY

The life history parameters growth, survivorship and fecundity were investigated in strains A and C of the clonal apomictic snail *Potamopyrgus jenkinsi*. Both strains were obtained from separate habitats. Strain A from an inland freshwater stream and strain C from a boating pond which receives seawater and is drained every winter.

When reared from birth in constant laboratory conditions the two strains were shown to differ in life history strategy. Strain C showed rapid growth, matured early and at a relatively small size. Hence it had greater reproductive effort. Strain A delayed growth, matured relatively late in its life history and hence at a larger size. The results in this work suggests that strain A and C are distinct clones, which support recent electrophoretic studies.

In manipulated environments of food stress and increased salinity the two strains continued to show significant differences. Both strains were plastic in their growth, reducing growth in response to decreasing food availability and high salinities. However at 5% and 10%SW the two strains showed an increase in growth from that of the control.

Their reproductive output also decreased with decreasing food supply and increasing salinity. However, strain A was more sensitive to food and salinity stress, ceasing to release young at low ration and starved environments and at salinities of 20%SW and above. Strain C continued to release young in all environments, albeit at a reduced rate and at a cost to survivorship.

A yearlong field study on the size-frequency distribution of the two strains in their natural habitat showed the life history of strain A to approximate 'K'-selection and strain C to approximate 'r'-selection.

This is dedicated to my mother and the late Mrs. Rapaport who was a great inspiration and remarkable lady.

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CHAPTER 1:

GENERAL INTRODUCTION

According to Darwin's theory of evolution, individuals possessing heritable traits that promote reproduction and competitive ability for finite resources such as food and space will tend to predominate in a population. Hence the fittest survive and the most successful traits become more common from one generation to the next. Natural selection as explained by Darwin, however, considers only the fitness of the individual and not of the gene (Sibly and Calow, 1986). This has lead evolutionary biology to be split into two main branches: population genetics (the most recent approach), concerned with the effect of natural selection on gene frequencies (Via and Lande, 1985; de Jong, 1990) and the adaptationist programme, which is concerned with the selective advantages that have given rise to particular phenotypes.

1.1 ADAPTATIONIST PROGRAMME

The adaptationist programme can be applied in two ways: the *a priori* approach, which considers the probable evolution of certain traits under specified ecological conditions and the *a posteriori* approach, which considers why certain traits have evolved in particular ecological conditions (Sibly and Calow, 1986).

Population geneticists criticise adaptationists for not understanding the genetic basis of the traits that they study (Rose *et al.*, 1987). Gould and Lewontin (1979) accused the adaptationist programme of being a "Panglossian paradigm", especially in its *a posteriori* approach (see Mayr, 1983). The "Panglossian" assumption, often implicit in this approach, is that all traits are adaptive and so can be explained by the hypothesis (Sibly and Calow, 1986). Nevertheless, the adaptationist's *a posteriori* approach is strengthened when observed traits change in populations of the same or related species occupying different ecological conditions (Sibly and Calow, 1986). For example, the physiology of *Patella vulgata* and *Patella aspera* differs as they occupy different levels of the shore: *Patella vulgata*, positioned on the upper shore, can survive higher temperatures than *P.*

aspera, positioned at lower levels (Davies, 1969).

Both branches of evolutionary biology agree that successful traits are those that maximise fitness. Fitness, however, usually depends on the combined effects of at least several factors, for example survivorship, fecundity and age of maturation. It is often not possible to maximise simultaneously all contributors to fitness because of constraints imposed. These constraints are the genetics, developmental physiology, demography and the ecology of the organism, together with competition among functions for the allocation of finite resources. Instead, the set of fitness-related traits is optimised as a result of natural selection. Optimality models tend to consider only the phenotype, ignoring any genetic constraints that may bear upon the evolution of the optimum phenotype (Maynard Smith, 1978).

1.2 PHENOTYPIC PLASTICITY

Phenotypic plasticity is a concept that unites the ecological and genetic approaches, described above. It was first proposed by Levins (1968) and has now been recognised as being not only a concept, but an important factor in evolution (Bradshaw, 1965; Lewontin, 1974). Thus, the plastic response of a phenotype to environmental change may facilitate the exploitation of a wide range of circumstances.

Plasticity is believed to be under genetic control (Dobzhansky, 1951; Khan *et al.*, 1976; Jain, 1978). Dingle *et al.* (1982) found that Puerto Rican and Iowa populations of the milk weed bug, *Oncopeltus fasciatus*, differed in their sensitivity to temperature. The differences were originally explained as being due to migratory and non-migratory strategy in the life history. But as pointed out by Stearns *et al.* (1991), the influence of phenotypic plasticity on the genetic covariance should have been considered in order to judge whether or not the plasticity is adaptive (Caswell, 1983; Thompson, 1991).

Once plasticity has been revealed as a significant genotype-by-environment interaction, its properties can be shown by a reaction norm (Schmalhausen, 1949). A reaction norm is the set of phenotypes expressed by a single genotype across a range of environments (Stearns *et al.*, 1991; Thompson, 1991).

1.3 CONSTRAINTS

Constraints acting on selection prevent the evolution of the perfectly adapted organism (Mayr, 1983). Such constraints are generally known as trade-offs and they form the basis of optimality models. In the context of life history, trade-offs arise from the principle of the conservation of energy (Sibly and Calow, 1986), which dictates that increased allocation to one trait is compensated by decreased allocation to another (Stearns, 1989a). Care must be taken when interpreting observed data, because compensation can have both a genetic and a non-genetic basis. The latter is known as ecological compensation (Maynard-Smith, 1978; Mayr, 1983; Sibly and Calow, 1986). Ecological compensation involves non-inheritable, phenotypic adjustments to allocation that promote population stability. It may influence genetically-based compensation by constraining the direction of evolutionary change and so should not be ignored (Sibly and Calow, 1987).

Mayr (1983) considered two kinds of ecological constraint on life-history evolution. One was the flexible phenotype, where no re-organisation of the genotype was necessary due to the ability of the phenotype to withstand changes in the environment. Wright (1931) and Stebbins (1950) considered that where such plasticity was present, it would reduce the impact of natural selection by reducing the selective differential between genotypes and thus retard evolutionary change (Levin, 1988). Thompson (1991), pointed out that phenotypic plasticity itself has a strong heritable nature and may actually aid further evolutionary change as shown by Jaenike (1978) for closely related plant species, thus should not be considered as a constraint on life-history evolution (Thompson, 1991).

The other ecological constraint on life-history evolution, or indeed on any other character set, is that of stochastic processes (Mayr, 1983), where unpredictable factors in the environment may prevent a deterministic outcome of selection pressures.

1.31 The allocation trade-off

Allocation of limited resources to one trait e.g. reproduction at the expense of another, such as growth, can result in conflict between investments. An important allocation conflict is the so-called "cost of reproduction", reviewed extensively by Stearns (1976; 1977), Reznick (1985) and Bell and Koufopanou (1986). Reproductive cost has two major components, the cost paid in parental survival and the cost paid in future fecundity. These negative effects become especially severe when resources are scarce.

1.4 MEASUREMENT OF CONSTRAINTS

There are two main approaches to measuring constraints in life-history, phenotypic and genetic. The phenotypic approach considers the adaptiveness of a trait when under selection pressure. The methods used in this approach are phenotypic correlation and experimental manipulation. The genetic approach considers the effects of selection on gene frequencies by genetic correlation and artificial selection. These methods have been reviewed by Stearns (1977), Reznick (1985), Bell and Koufopanou (1986) and are outlined below.

1.41 Phenotypic correlation:

The correlation between two life-history traits is measured. For example, reproductive effort and its potential cost to the parent in terms of growth or survivorship. Thus, from the principle of energy allocation, one would expect a negative correlation. However, observations have often shown them to be positive (Rose and Charlesworth,

1981), especially when measurements are made on individuals within populations (Bell and Koufopanu,1986).

It should be remembered that when measured under favourable conditions, phenotypic correlations can provide no decisive evidence for the cost hypothesis (Bell and Koufopanou, 1986). Phenotypic correlations are no longer considered to be suitable for the measurement of cost (Reznick, 1985; Bell and Koufopanou, 1986; Lessells, 1991). This is due to the lack of adaptive variation in allocation under favourable condition (Bell and Koufopanou, 1986), and the failure of phenotypic correlations to consider individual differences in resource requirement and allocation schedules.

1.42 Experimental manipulation:

This can either be direct or indirect. Direct manipulation focuses on some particular aspect of the life history. A life-history character is measured by the response to experimentally induced changes. For example Partridge and Farquhar (1981) measured reduced longevity resulting from experimentally increased sexual activity in male *Drosophila melanogaster*. In appropriate cases, direct manipulation reveals the degree of phenotypic plasticity (Reznick, 1985).

Indirect manipulation focuses on some critical aspect of the environment, for example food availability. In this way two or more life-history variables can be measured and then correlated. Here again, problems may arise because the manipulated environment itself can cause the change observed, independently of any allocation trade-off (Reznick, 1985; Bell and Koufopanou, 1986; Sibly and Calow, 1986; Lessells, 1991).

1.43 Genetic correlation:

Genetic correlation involves the locus or loci which determine the allocation of resources that will affect both traits. Thus a genetic increase in allocation to one will lead to a genetic decrease in allocation to the other. This is also known as antagonistic pleiotropy (negative genetic correlation, Lande, 1982). However, positive correlations, rather than negative, are usually observed (Stearns *et al.* 1991). Such positive correlations are believed to be caused by the creation of inferior genotypes by inbreeding or mutation,

which results in low survivorship and fecundity (Rose, 1984).

1.44 Artificial selection:

One life-history component is selected by a breeding programme and the concurrent response of another component, not under selection pressure, is measured. This technique, however, has met with varied success (see Bell and Koufopanou, 1986). Although selection experiments tend to yield a greater proportion of the predicted negative correlations than the technique of genetic correlation (above), very large samples sizes are needed in order for the results to be a reliable indication of trade-offs (Bell and Koufopanou, 1986; Lessells, 1991).

There is current debate as to whether the phenotypic or genetic approach is preferable for interpreting life histories. Reznick (1985) argues that genetic analysis is of greater evolutionary significance, since only genetically coded options can take part in the evolutionary processes. However experiments have shown (eg. Møller *et al.* 1989b) that where a negative correlation had been created by manipulation, the corresponding estimated genetic correlation proved to be positive, suggesting that there were no trade-offs between the two traits. According to Bell and Koufopanou (1986) experimental manipulation, if well designed, usually gives consistent results that provide empirical data suitable for testing hypotheses about trade-offs. In contrast, genetic correlations tend to be misleading because culturing and isolation of individuals themselves may influence, in some unknown way, the covariances that should be measured. Thus genetic correlations should be treated with caution (Stearns, 1989a).

Genetic variation among populations can be assessed at the phenotypic level by applying a common environment, or "common garden" approach, which eliminates any environmentally induced differences (Bradshaw, 1984; Calow, 1981; Ouborg *et al.*, 1991). Interpretation of common-garden experiments can be hampered by maternal carry-over effects (Lam and Calow, 1990; Ouborg *et al.*, 1991).

Another way of studying the effects of genetic variation is to conduct transplant experiments, where individuals from different populations are reciprocally transferred between their respective habitats (e.g. Breven, 1982; Brown, 1985). However, as experimentally demonstrated by Lam and Calow (1990) and pointed out by Sibly and Calow (1986), the performance of progeny, in addition to that of the transplanted organisms themselves, needs to be observed so that heritable differences can be verified.

Organisms used in the measurement of trade-offs are generally sexual individuals. Therefore in order to select for different traits, the genotypic differences need to be averaged out by choosing a large sample size and allocating individuals at random to different manipulations. Ideally, genetically identical individuals from a clone should be used in order to distinguish the evolved from the ecological response (Møller *et al.*, 1989b).

1.5 REPRODUCTIVE STRATEGIES

Of great importance to evolutionary theory are the reproductive strategies adopted by organisms. There are two principal methods of reproduction: sexual and asexual. Sexual reproduction involves recombination and segregation, giving rise to progeny that are genetically variable. Asexual reproduction involves either somatic division through fragmentation, fission, or budding, or parthenogenesis, the development of unfertilised eggs. There are two types of parthenogenesis. Automictic parthenogenesis can be of various forms, depending on the way in which diploidy is restored before or after meiosis (White, 1973). Most forms of automixis increase homozygosity and so may be regarded as a form of inbreeding, in which deleterious recessives may be rapidly exposed to selection.

The most common form of parthenogenesis is apomictic. Here there is no meiotic division of the egg and, due to the absence of recombination and segregation, a highly fit genotype can be maintained and replicated (Johnson, 1981). Apomictic parthenogenesis

therefore is free from genetic load and replication of the genome is affected only by mutation, which is slow, especially in polyploid organisms (Johnson, 1981).

The advantages and disadvantages of sexual and asexual reproduction have been discussed by many authors (Fisher, 1930; Muller, 1932; Eshel and Feldman, 1970; Felsenstein, 1974; Hughes, 1989).

Fisher (1930) and Muller (1932) established the classic theory on the evolution of recombination (Felsenstein, 1974). According to the Fisher-Muller theory, a recombinant population can evolve faster than a non-recombinant population. One reason for this is that favourable mutations arising in different individuals can eventually be combined into the same genome, which otherwise would be most unlikely to acquire both through chance mutation alone. The Fisher-Muller theory, however,has been the source of much controversy (Crow and Kimura, 1969; Maynard Smith, 1968; Eshel and Feldman, 1970). Maynard Smith (1968); Eshel and Feldman (1970) found from their models that recombination has no effect on gene frequency and hence the rate of evolution. However, Felsenstein (1974) in his review showed that models based on finite populations predicted recombination to be advantageous, while those based on infinite populations found no such advantage. Nevertheless, sexual reproduction is present in the great majority of multicellular eukaryotes, even though there is a cost in having males relative to all-female reproduction (Williams, 1975; Maynard Smith, 1978). However, this is due to the need of low linkage-disequilibrium for recombination to have an effect.

The Fisher-Muller theory implicitly invoked group selection, which has recently been rejected (Maynard Smith, 1978; Bell, 1982). More recent models have sought a short-term, individual advantage to sex (Glesener, 1979; Hamilton, 1980; Bell, 1982; Rice, 1983). The majority of short-term models emphasise the benefits of phenotypically variable progeny in temporally or spatially variable environments (Bell 1982). Indeed the "Tangled Bank" hypothesis (Bell, 1982; 1985) assumes spatially heterogeneous environments to maintain sexuality and that habitats consist of an array of resource type

which no individual phenotype is capable of exploiting completely (Weeks and Sassaman, 1990). In models such as this, the lack of genetic variability of asexual reproduction is predicted to be disadvantageous relative to the genetic diversity created by sexual reproduction (Vrijenhoek, 1979).

Workers are once more starting to pay attention to group selection (Gliddon and Gouyon, 1989; and Nunney, 1989). Gliddon and Gouyon (1989) point out that while most evolutionary biologists are prepared to agree that the fitness of the individual is determined at the molecular level and hence fixed, the same reasoning should be given to group selection. Thus group selection is the process of selecting those groups in which individual selection has had the most beneifical effect at the group level. Nunney (1989) explains the maintenance of sex by group selection. In his model he incorporates the short term disadvantage of sex (i.e. the production of males) by assuming that asexual individuals arising from mutation in a sexual species will rapidly displace the sexual individuals. Thus the species will eventually become asexual. The probability that this will occur is given by the transition rate, u_s. If this value varies among lineages then one of the effects of group selection is to favour the group (i.e. species) with the lowest u_s value. This is because those (groups) that are asexual have a high extinction rate because of a high u_s value. Hence in the long term only those that do not convert to asexuality (because of a low u_s) survive hence maintaining a large proportion of sexually reproducing species.

The absence of recombination is usually believed to decrease the rate of adaptive evolution and speciation and to increase the rate of extinction (Fisher, 1930; Muller, 1932; White, 1978). However, many parthenogenetic species (e.g. anholocyclic aphids, weevils and some fishes) are successful and are widely distributed geographically.

Hughes (1989) concluded that the advantages of cloning are short-term, for without sex, the evolution of purely clonal lineages is probably slow. The short-term advantages of parthenogens relative to equivalent bisexual lineages include their higher population growth rate, greater colonizing ability (Gerritsen, 1980), and freedom from the cost of males (Maynard Smith, 1978). Genetic benefits of clones include the increased

heterozygosity and the continuation of fit genotypes (Bell, 1982). Selection in clonal populations may even enhance evolutionary adaptation to local environmental conditions (Bell, 1982) due to non-additive genetic functions (Eshel and Feldman, 1970). In the case of colonisers a "general purpose genotype" may evolve (Baker, 1965).

Much interest has recently arisen in the use of clonal organisms for the experimental investigation of evolutionary problems concerning reproductive and other life-history characteristics (e.g. Møller *et al.*, 1989b; Stearns, 1985; Hughes, 1989). Clonal animals enable some of the practical problems encountered in experimental manipulation to be overcome. As mentioned above, life-history traits are under genetic and environmental control. Because individuals within a clone are genetically identical, each genome can be replicated and exposed to different treatments. It should therefore be possible to distinguish between the genetic and environmental contributions to the variance of life-history traits (Hughes and Hughes, 1986).

1.6 THE DISTRIBUTION AND BIOLOGY OF *POTAMOPYRGUS JENKINSI*

Potamopyrgus jenkinsi was first described by E.A. Smith (1889), from specimens found in the Thames estuary, but was probably introduced as early as 1859 (Hubendick, 1950; Frömming, 1956). Since this sudden appearance, the distribution of *P. jenkinsi* has extended throughout continental Europe (Lucas, 1959; Réal, 1973). Its rapid dispersal has been well documented (e.g. Bondesen and Kaiser, 1949; Hunter and Warwick, 1957; Warwick, 1969; Wallace, 1985).

Since its discovery, the origin of *P. jenkinsi* has been the subject of much discussion. Bondesen and Kaiser (1949) reviewed two theories. The first was that *P. jenkinsi* arose by mutation from *Hydrobia ventrosa* (Steusloff, 1927) and the second was that it originated from another, non-European country (Bondesen and Kaiser, 1949).

Bondesen and Kaiser (1949) suggested *P. jenkinsi* to have originated from Australia, noting that it is very similar to examples of *Austropyrgus pattisoni.* Boettger (1951) suggested a New Zealand origin, as he considered the shell characteristics of *Potamopyrgus jenkinsi* to be identical to those of the native *Potamopyrgus antipodarum.*

Winterbourn (1970, 1972), also, compared the characteristics of *P. jenkinsi* to those of *P. antipodarum* and suggested that the colonisation of inland waters from estuaries by *P. jenkinsi* in Europe parallelled that of *P. antipodarum* in New Zealand. However, the morphological variation in *P. antipodarum* is greater than that in *P. jenkinsi* and is considered to be due to the greater genetic divergence that has occurred over a long period of time and to sexual reproduction that occurs in some populations of *P. antipodarum* (Winterbourn, 1972).

Warwick (1952) showed the shell morphology and body pigmentation of *P. jenkinsi* to be of three distinct types. He called these strains A, B and C. Warwick (1952) generally found that populations consisted only of one strain, although two or three strains could sometimes coexist. The most common strain, strain A (Warwick, 1952; Simpson, 1976) is slender in shape and its mantle pigmentation is pale with transparent stripes along the length of the tentacles. Strain B is much shorter and fatter and its pigmentation is almost black. In strain C, shell shape is intermediate between those mentioned above and the otherwise smooth periostracum sometimes bears a keel, which has attracted much attention (Robson, 1926; Boettger, 1948; Warwick, 1952). Strain C is generally mottled in pigmentation, with a dark spot behind the eye on the dorsal surface of the tentacle.

The presence of three distinct strains in Europe has led authors to consider splitting *P. jenkinsi* into separate species (Mayr, 1963; Warwick, 1969). However, the parthenogenetic nature of *P. jenkinsi* presents taxonomic difficulties. Mayr (1963) stated that subdivision into three species is justifiable on the basis of differences in shell shape, pigmentation, ornamentation and distribution. Moreover, Todd (1964) showed there to be physiological differences between the strains. Another argument in favour of Warwick's (1969) proposal for subdividing *P. jenkinsi* was the fact that it is rare for two or three of the

strains to coexist. Winterbourn (1972) thought it debatable as to whether the strains were distinct enough to warrant formal recognition, as suggested by Warwick (1969). Winterbourn (1972) found from shell measurements, a continuous variation in shell shape from stout to slender. The considerable variation in pigment intensity occurred between, as well as within, populations and was poorly correlated with shell form. Thus Winterbourn (1972) suggested strain B to represent one extreme phenotype in a variable series. More recently Johnson (1981) and Foltz *et al.* (1984), using electrophoretic methods, found *P. jenkinsi* to be comprised of the three strains described by Warwick (1952), with strain B and C being more similar to each other than to strain A, which was found to be more similar to *P. antipodarum*. Hauser *et al.* (1992), using DNA fingerprinting, have also shown the three strains around Britain to be consistently distinct.

P. jenkinsi is viviparous and parthenogenetic. Its parthenogenetic mode of reproduction was first discovered by Boycott (1919) and confirmed by Quick (1920) and Robson (1923). Sanderson (1940) considered *P. jenkinsi* to be made up of two races: diploid in Europe (2n=20-22) and tetraploid in Britain (36-44). Recently, Wallace (1992) has shown that both New Zealand apomictic individuals of *P. antipodarum* and European *P. jenkinsi* probably are modified triploids, with sets of 46 or 52 chromosomes. *P. antipodarum*, although frequently apomictic (Winterbourn, 1970), produces males that have a sexual function in certain populations and produce normal, haploid sperm.

Because *P. jenkinsi* is parthenogenetic, no males are expected to be found. However, a single male was found by Patil (1958), since then other, sporadic cases have been recorded. Wallace (1979, 1985) found the occurrence of males in *P.jenkinsi* to be most widespread in North Wales, in the region of Harlech. However none were found in the present study.

1.7 AIMS

The present study was designed to investigate the genetic and environmentally induced components of phenotypic variation within and between strains A and C of *P. jenkinsi*. Genetically determined differences in life-history strategy were assessed by rearing the strains under constant laboratory conditions (chapter 2). Environmentally-induced phenotypic variation (plasticity) was studied by placing the two strains under several levels of food stress (chapter 3) and salinity (chapter 4). Because *P. jenkinsi* is parthenogenetic, it is predicted to have a general-purpose- genotype (Baker, 1965). The generality in genotype of the two strains as an explanation of colonisation pattern is considered (chapter 5).

1.8 GENERAL METHODS

1.81 Collection

The two strains A and C were collected from two different sites, where they were found in abundance and in almost exclusion of the other strain.

Strain A was collected from Llansadwrn stream, Anglesey, (SH 551767), while strain C was collected from the boating lake at Llanfairfechan (SH 678754).

The snails were collected either by removing them from rocks with a fine artist's paint brush or by kick-sampling into a net for one minute. The net contents were then sifted and the snails removed.

1.82 Maintenance

The snails were housed in large tanks measuring 30cm by 15cm by 7cm. The water used in the stocks and in the experimental containers was an equal mixture of copper-free tap water and twice-filtered pond water. The water in the experimental containers was

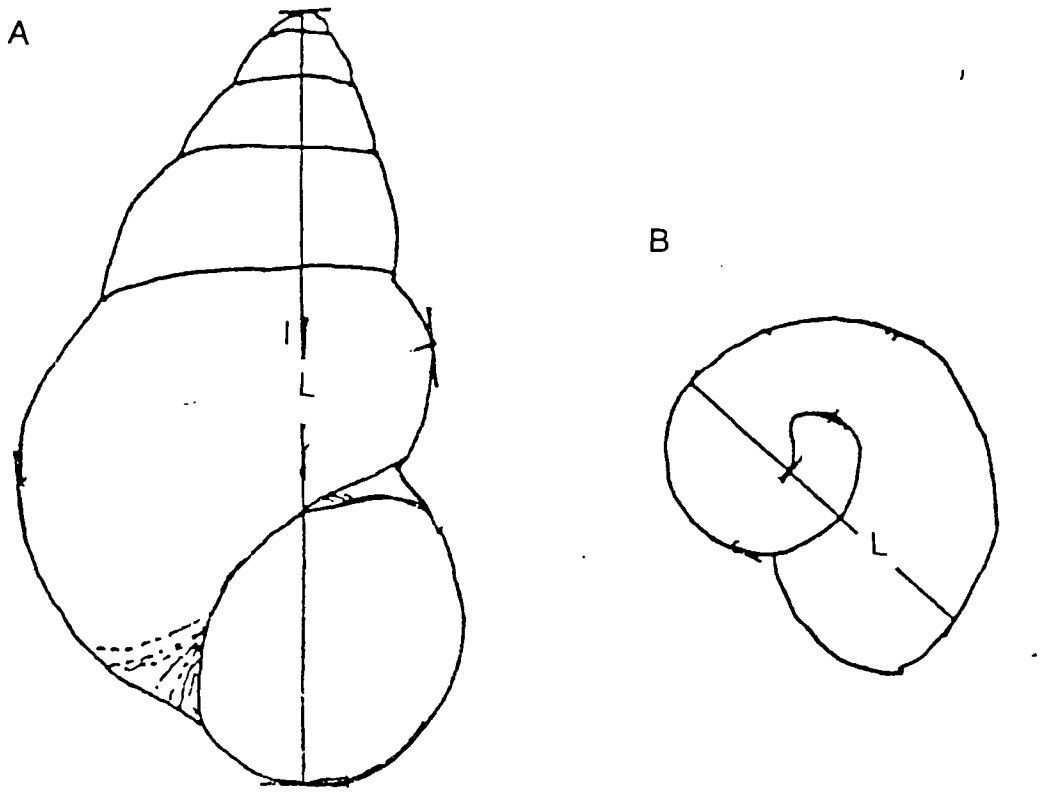

Figure 1.1: A) Shell length was measured from apex to base of shell in adults and large juveniles. B) Newly released juveniles were measured along the length of the shell.

changed every 7 days. When cleaned, the sides would be wiped with a cloth to remove any algae that may have formed. Each time the water was changed, a drop of hardener was added. The hardener consisted of: 50g calcium carbonate, 5g magnesium carbonate, 5g sodium chloride, 1g potassium chloride, 3l copper-free water (Malek and Ching, 1974). This was used initially to strengthen the shells and so make them easier to handle. The stock containers were not cleaned during routine maintenance as the build up of microflora provided additional food source.

The snails were fed on sycamore, *Acer pseudoplatanus*, leaves. The leaves were collected in spring, air-dried and stored until needed. Before use, the leaves were soaked for at least 48 hours to remove excess tannin. Originally, boiled lettuce was tried as it had commonly been used by other workers (e.g. Johnson, 1981).
However, a high mortality rate was noted each week and the water became discoloured very quickly. The use of sycamore leaves was justified from Hanlon's (1981) previous success in rearing *P. jenkinsi* on this food.

1.83 Measurement of shell length

The growth of large juvenile and adult snails was measured by recording the shell length from the apex to the base of the aperture (Figure 1.1a). Newly released juveniles were measured along the length of the shell as shown in Figure 1.1b. Using an eye graticule in a binocular microscope, measurments were initially made in eye units and converted to mm by the equation

mm = eu * 6.2/10

Where:

10 = microscope magnification

eu = eye units

6.2 = the number of eye units to 1 mm.

CHAPTER 2:

LIFE HISTORY STRATEGY OF STRAINS A AND C IN CONSTANT LABORATORY CONDITIONS

SUMMARY

Life history parameters (growth rate, fecundity and survivorship) were measured in strain A and C when reared from birth in constant laboratory conditions. Significant differences in growth schedule, size at maturation and fecundity were shown between the two strains. Strain C showed rapid growth, matured early and in doing so released more young. Strain A delayed growth and matured relatively late in its life and at a large size, hence showing lower reproductive effort.

The results obtained support electrophoretic studies suggesting that strain A and C are distinct clones.

2.1 INTRODUCTION

Intraspecific life-history variation usually is assumed to be the result of natural selection producing local adaptive traits. Stearns (1976) summarised the proposed selection forces, and discussed how they are predicted to produce covariation in life-history traits. Variation may be due to environmentally induced phenotypic changes, such as developmental plasticity or physiological acclimation (Stearns,1980). Intraspecific life-history variation (or the lack of it) may be due to phylogenetic constraints caused by past evolutionary history. For example Calow (1978) suggested that egg size may be phylogenetically limited in freshwater prosobranchs.

It is clearly advantageous, therefore, to determine the degree of genetic control of intraspecific life-history variation. The relative importance of genetic and environmental factors can be shown through reciprocal transplant experiments, in which individuals are transferred among habitats. Performance of the transplants is compared with that of the residents and may be compared among successive generations after transplantation. Brown (1985) found intraspecific variation to disappear after two generations when *Lymnea elodes* was reared in a constant environment. Much of the initial intraspecific variation seen was as a result of phenotypic plasticity. However, Breven (1982) found a large, proximal component to intraspecific life-history variation in ranid frogs, correlated with temperature variation among ponds at different altitudes. Frogs from higher altitudes still grew more rapidly than those from lower altitudes even in the same pond, suggesting genetic adaptation produced by "counter-gradient selection". Similarly Brown, De Vries and Leathers (1985) found that while proximal factors accounted for most of the intraspecific variation in *Lymnea elodes,* there was some genetic divergence between populations from vernal ponds and those of permanent ponds.

The life history of an organism reflects conflicting demands on the energy budget, as investment in one function often necessitate less in another. For example, a consequence of reproducing early may be a relatively small adult size. Consequences of

having many offspring may be a reduced adult life span and reduced survivorship per offspring. These are known as Trade-Offs (Bell and Koufopanou,1986; Stearns,1989a) and can occur between any pair of life-history traits. Two predominant trade-offs are first, between current reproductive effort and future resource investment (Stearns,1977; Bell and Koufopanou,1986). This not only uses up the resources of the parent and so affects future reproduction, but can also reduce the parent's life span. The second trade-off is between the number and survivorship of the offspring; the more that are produced, the smaller they will be and the less likely they are to survive. The traits used to study trade-offs, therefore, include longevity, age of first reproduction, somatic growth rate, and size at maturity.

The General Introduction (chapter 1) discusses the genetic and phenotypic approaches to measuring life history. The phenotypic approach is achieved either by phenotypic correlations (Bell,1984), where reproductive effort is correlated with a potential cost, or by experimental manipulation, where one trait is altered and the response of another is measured Reznick (1985).

The second approach is genetic analysis (Via and Lande,1985; de Jong,1990), which is achieved either by estimating genetic correlations between components or by artificial selection experiments in which one component is selected for and the concurrent response of the other is measured.

The phenotypic approach was used in the present study. The objective was to examine the life-history strategy and trade-offs between traits of the two strains A and C of *Potamopyrgus jenkinsi* when cultured under constant feeding and temperature conditions from birth to death. The traits studied were growth, survival, parental size at first release of young.

The snails used in this study were bred from stocks whose ancestors had come from different habitats. Strain A was collected from a freshwater stream (Llansadwrn, SH 551767) while strain C was collected from a pond (Llanfairfechan, SH 678754) that had

inputs both from the sea and from an adjacent river , and so was brackish. It was also an unstable environment, for in winter the pond is drained, leaving only residual seawater and rain water. Therefore, strain C is from a less predictable and strain A from a more predictable environment.

2.2 MATERIALS AND METHODS

2.21 Rearing

Strain A and C snails from laboratory stocks were allowed to mature and release young. From each strain, eighty eight offspring not measuring more than 0.53mm, S.E = 0.056mm for strain A and 0.57mm, S.E.= 0.057mm for strain C, were placed in individual, clear plastic containers measuring 15cm by 7cm by 5cm. These juveniles were then reared in a C.T. room at a temperature of 12^0 C for 54 weeks with a continuous food supply of sycamore leaves as described in chapter 1.

2.22 Growth

Growth was recorded every 14 days by measuring the shell length, using a binocular microscope as described in chapter 1 (graticule calibrated to mm).

Statistical comparisons of the growth rates and the final mean length (mm) of the snails were made with MANOVA (SPSS). MANOVA is a generalised procedure for analysis of variance and can be used for the analysis of repeated measures. A repeated measures analysis allows an analysis of variance to be performed at each time intervals to demonstrate differences between the strains (SPSS Manual).

2.23 Survivorship

Every 14 days, dead snails were counted and removed from the containers. Differences in survivorship between the two strains were compared using Survivorship

Analysis (SPSS) and the Lee-Desu statistic. This analysis produces life tables (appendix 2), listing the proportion surviving and its standard error at the end of each time (14 day) interval, together with the cumulative proportion surviving and the median survival time. The Lee-Desu statistic (Lee & Desu, 1972, cited from SPSS Manual) compares the survivorship of the two strains using the D-statistic. This is calculated from the survival scores using the alogorithm of Lee & Desu (1972). The larger the D-statistic the greater the probability of significant difference.

2.24 Fecundity and size at first release of young

The number of young released by each individual every 14 days was recorded. Also recorded was the shell length at which the snails first released young. ANOVA (MINITAB) was used to reveal any significant differences in the fecundity and size at maturity between the two strains.

2.25 Length-Weight Curves

Originally, a histological study was to have been carried out to ascertain the relative allocation of energy reserves among organs in the body. However, sample sizes from the laboratory populations proved to be too small for this purpose. In order to obtain a crude measure of resources allocated to reproduction at the expense of growth, length-weight curves of both strains were produced. From these, it was possible to estimate the relative biomass attributable to somatic production, eggs and embryos

Between 50 and 100 snails each of strain A and C were taken from their original field habitat. The length (as described in 2.22) and total flesh weight was measured. Normally, in measuring flesh weight, the body is removed and then weighed. However, because of their small size (maximum shell length = 5mm), it was not possible to extract the flesh. Instead it was decided to weigh the snails in their shell, then dissolve out the flesh with TCPK-treated trypsin. Depending on their size, snails would be kept in trypsin

from between 6 to 24 hours. In order to help remove the flesh, the snails were agitated using an ultra-sonic vibrator for up to 30 seconds. The shells were then dried in an oven at temperature of 60°C and reweighed to find the body mass by subtraction.

Snails measuring 2mm or more were weighed on a Sartorius scale balance accurate to within 0.1mg. Snails measuring less than 2mm, or even larger sizes when dried, were too light to be recorded on the scale balance were weighed to within 25 μg using a C-31 Cahn electro-balance.

The relationship between shell length and dry flesh weight was investigated using linear regression analysis (method of least squares).

2.3 RESULTS

2.31 Growth

Growth curves for strains A and C are shown in Figure 2.1. Only individuals surviving the whole length of the experiment were included in the final analysis and production of the growth curves. The two strains had similar growth trajectories in the first four weeks. However, from week 6 to week 28, not only did the two strains grow differently, strain A showing a sigmoid growth curve and strain C a monotonic curve, but growth rate of strain C was greater than that of strain A. This was confirmed by the MANOVA (Table 2.1), which showed not only the shape, but also the growth rate to be significantly different (MANOVA, $F_{2,87}$= 16.85, P = 0.000). After week 28 strain C showed a reduction in growth. Strain A, however, continued to show linear growth until week 40, when it had reached the same shell length as strain C. Thereafter, strain A snails became significantly larger than strain C snails. (Table 2.1)

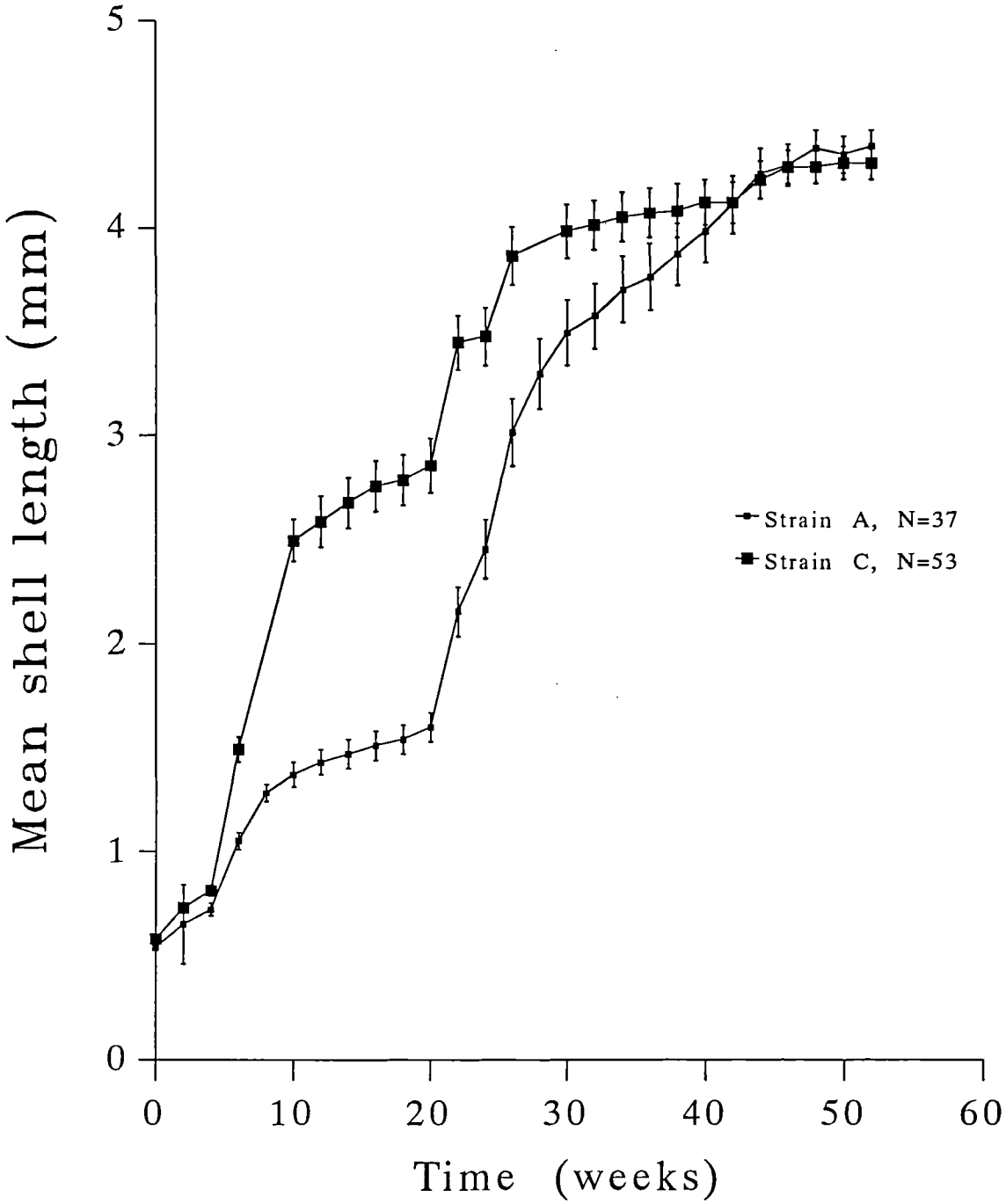

Figure 2.1: Growth curves of strain A and C under constant laboratory conditions from birth. Values are means, vertical lines standard errors.

Table 2.1: MANOVA (SPSS) showing variation between the two strains growth and final mean shell length with time. MANOVA test between-subjects effects. Only those snails that survived the whole length of the experiment (52 weeks) were used in the analysis.

Source of Variation	SS	MS	D.F.	F	P
STRAIN	149.17	149.17	1	16.85	0.000
ERROR	770.25	8.85	87		

Multivariate tests of significance:

EFFECT.. STRAIN BY TIME

Test Name	Value	Exact F	Hypoth. DF	Error DF
WILKS	.42950	3.34725	25.00	63.00

EFFECT ...TIME

WILKS	.01006	247.95473	25.00	63.00

Note..F statistics are exact.

2.32 Survivorship

The survivorship of the two strains was not significantly different (Figure 2.2, D-statistic = 2.02, D.F. = 1, P = 0.1553), although the median survival time, calculated from the life tables (see appendix 2, section 2.1) of strain C (54 weeks) was greater than that of strain A (50.3 weeks).

The mortality of both strain A and C was greatest in their juvenile period (Figure 2.3). The juvenile period of strain A, being longer than in strain C, was associated with greater cumulative mortality. By comparison, strain C had a relatively constant mortality rate between juvenile and adult phases.

2.32 Fecundity

The temporal pattern of fecundity (Figure 2.4) for both strains was similar, peaking at the same time (week 44). ANOVA performed on total fecundity showed there to be no significant difference between the two strains (Table 2.3). Throughout the 54 weeks of the experiment, the total number of young released by strain C per week was greater than in A (Figure 2.4). This was because strain C matured earlier and therefore its population contained more individuals releasing young. For example in week 34, 66.7% of strain C snails were releasing young while only 18% of strain a snails were releasing young. However, after the reproductive peak (week 44) the number of young released per individual (Figure 2.5), was greater in strain A than in strain C, although this difference was not statistically significant (Table 2.4).

The shell length at which the snails commenced releasing young differed significantly between strains A and C (Figure 2.6, Table 2.5). Strain C snails began to release young at a smaller size than strain A snails. The difference in the size at maturity is linked to the body mass predicted from the length-weight curves (Figure 2.7) and to the growth rate. Thus strain C grew faster than strain A and matured at a smaller size. Correspondingly, strain C matured at a significantly earlier age than strain A (ANOVA, $F_{1, 10} = 6.71, P = 0.027$).

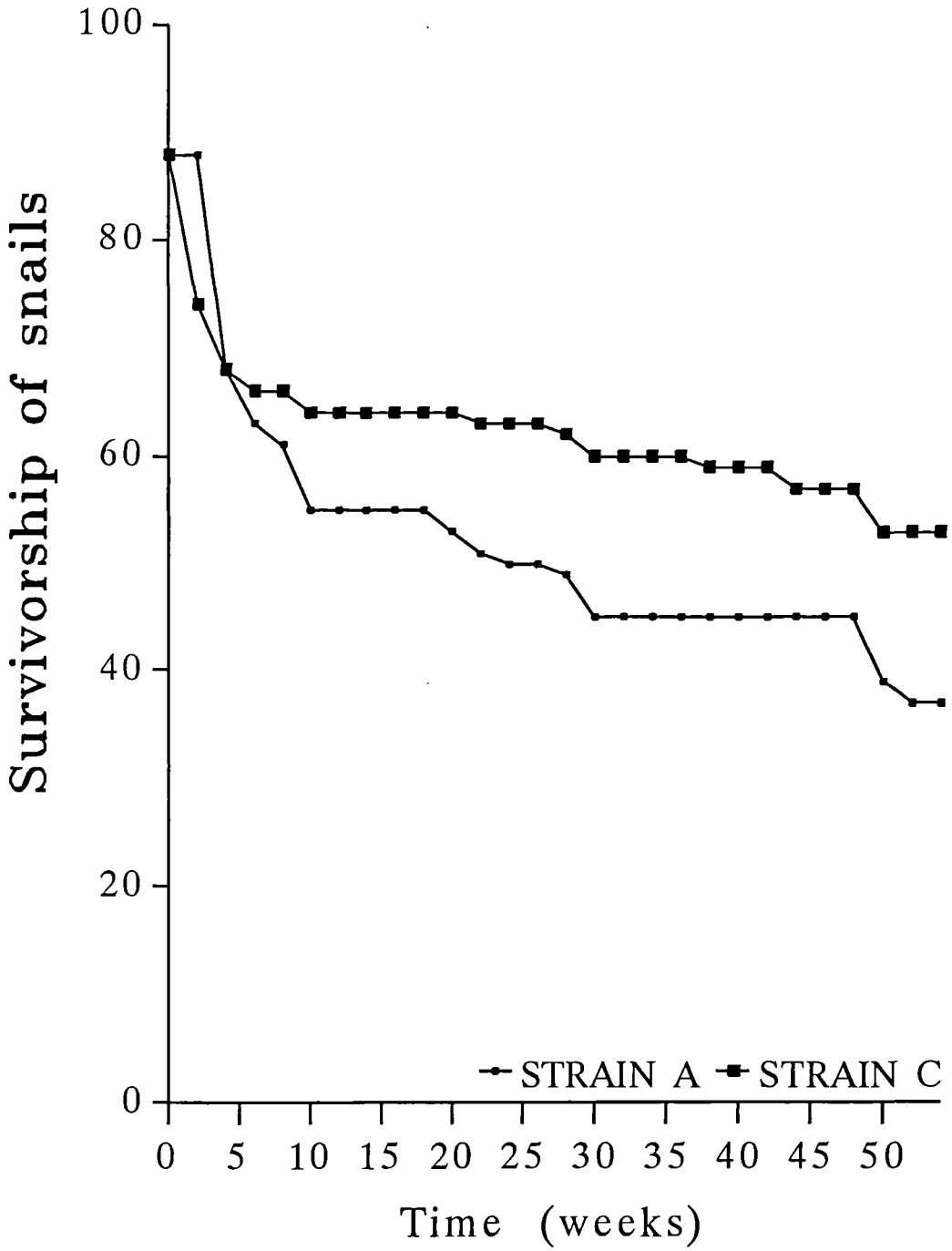

Figure 2.2: Survivorship curves of strain A and C from birth, in constant laboratory conditions.

Table 2.2: Survival comparison between strains A and C using the Lee & Desu statistic. At the start of the experiment there were 88 individuals.

Overall Comparison Statistic (D) = 2.02 D.F.= 1 P = 0.153

Strain	Total Number Dead at the end of Expt.	Total Number alive at the end of Expt.	% Dead
A	51	37	42.05
C	35	53	60.23

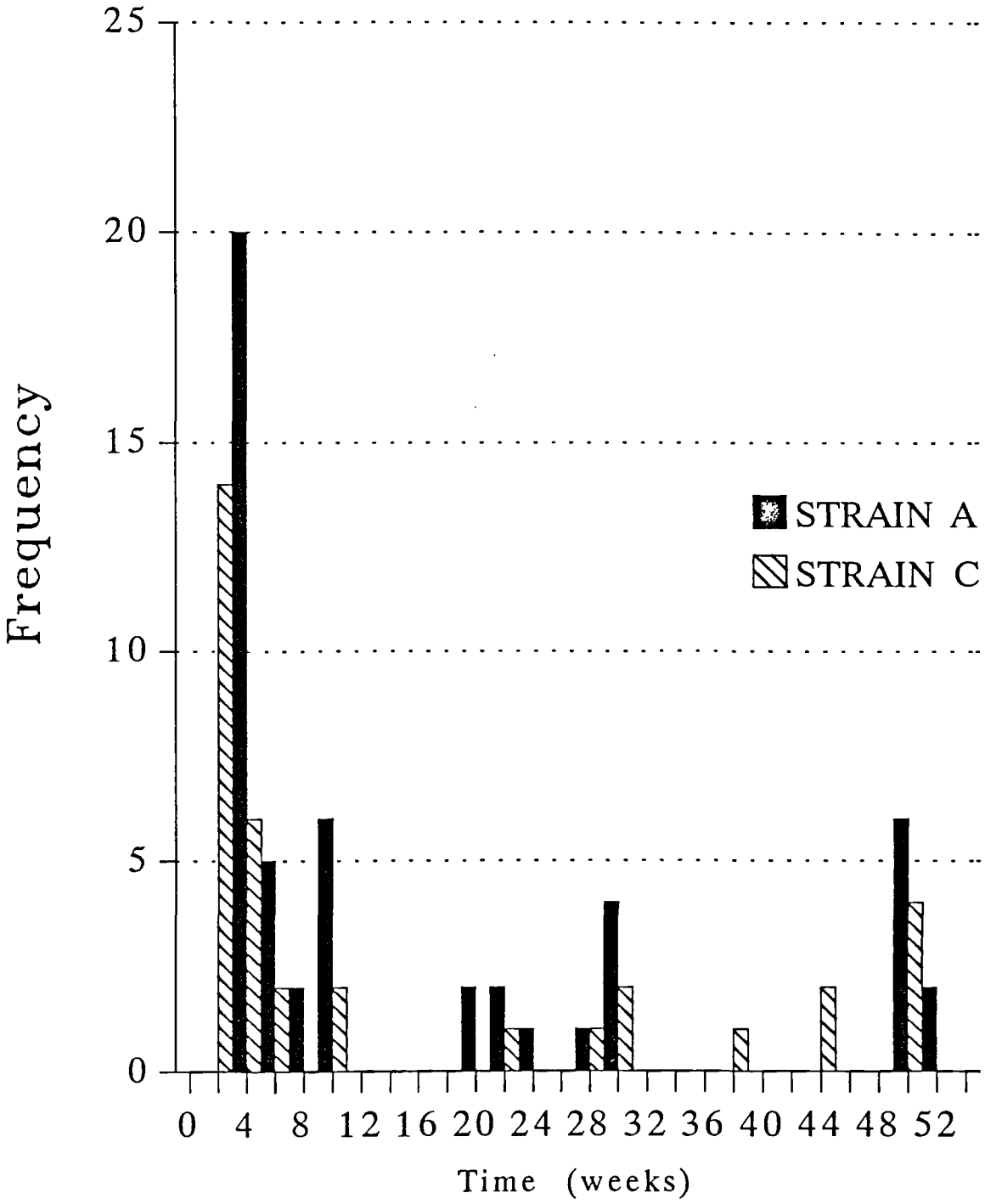

Figure 2.3: Weekly mortality of strain A and C snails in constant laboratory conditions

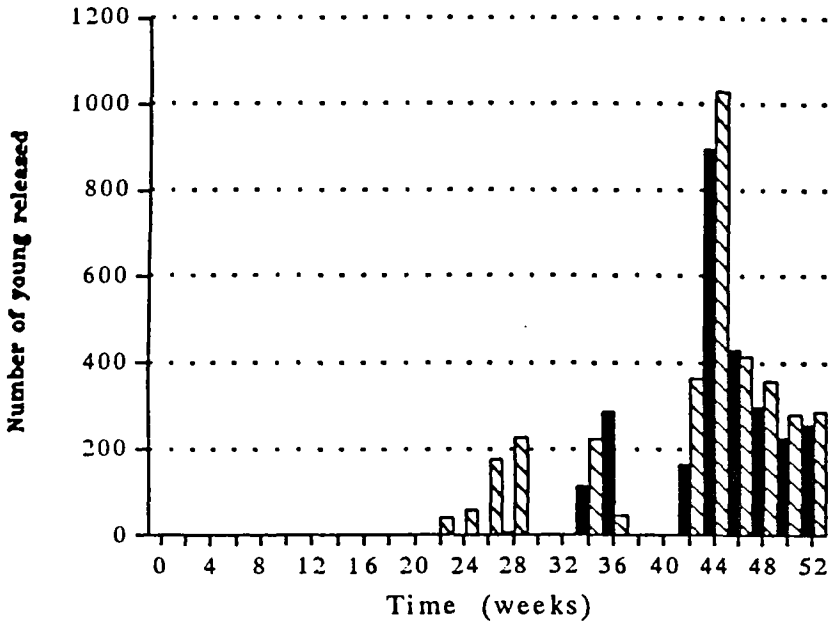

Figure 2.4: Total fecundity of strain A and C snails in the number released every 14 days.

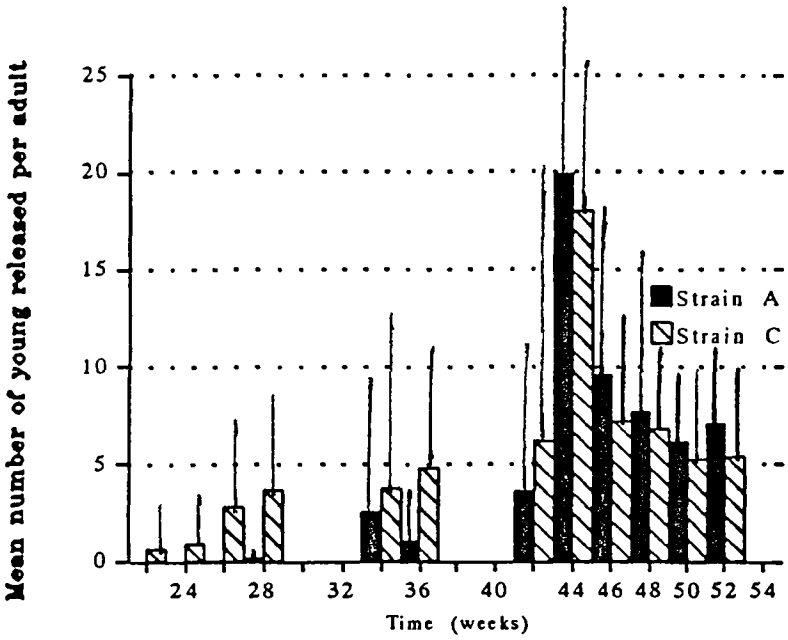

Figure 2.5: Mean number of young released per adult in strain A and C snails Each value is a mean, vertical lines standard errors.

Table 2.3: ANOVA of the total fecundity of strain A and C in optimal laboratory conditions.

SOURCE	SS	MS	D.F.	F	P
STRAIN	3186	3186	1	0.05	0.831
ERROR	1368777	68439	20		
TOTAL	1371963		21		

Table 2.4: ANOVA of the number of young released per snail of strain A and C in optimal laboratory conditions.

SOURCE	SS	MS	D.F.	F	P
STRAIN	0.57	0.57	1	0.02	0.886
ERROR	542.62	27.13	20		
TOTAL	543.19		21		

Table 2.5: ANOVA on the size (shell length, mm) at which the two strains first release young in optimal laboratory conditions.

SOURCE	SS	MS	D.F.	F	P
STRAIN	2.01	2.01	1	7.43	0.008
ERROR	18.13	0.27	67		
TOTAL	20.14		68		

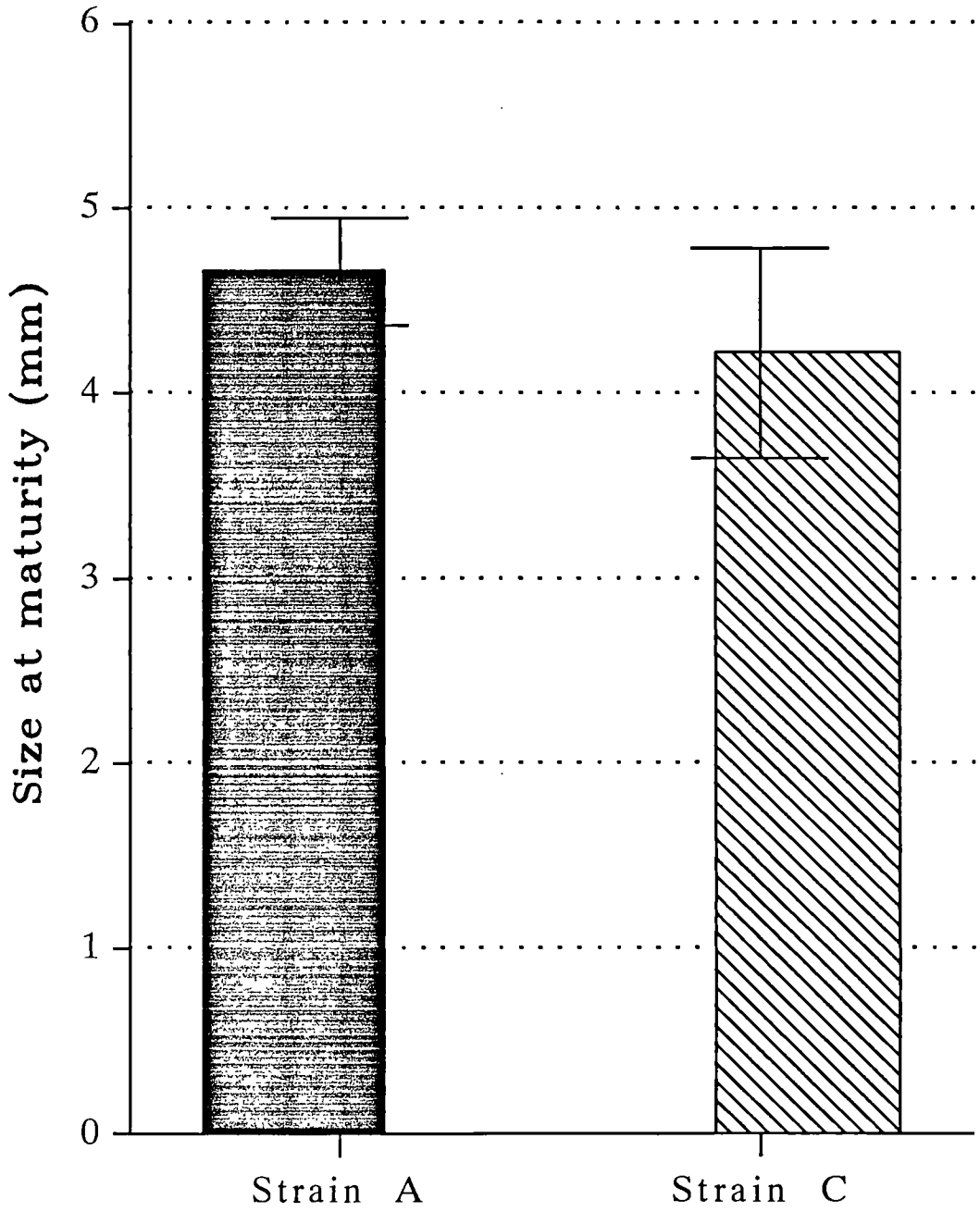

Figure 2.6: Mean size at maturity (in mm) for strain A and C snails when reared under constant laboratory conditions. Data are means plus or minus one standard error of the mean. Maturity was taken as the inital release of young.

Table 2.6: ANOVA of the age at maturation in strains A and C snails under optimal laboratory conditions.

SOURCE	SS	MS	D.F.	F	P
STRAIN	404.15	404.15	1	6.71	0.027
ERROR	602.51	602.25	10		
TOTAL	1006.67		11		

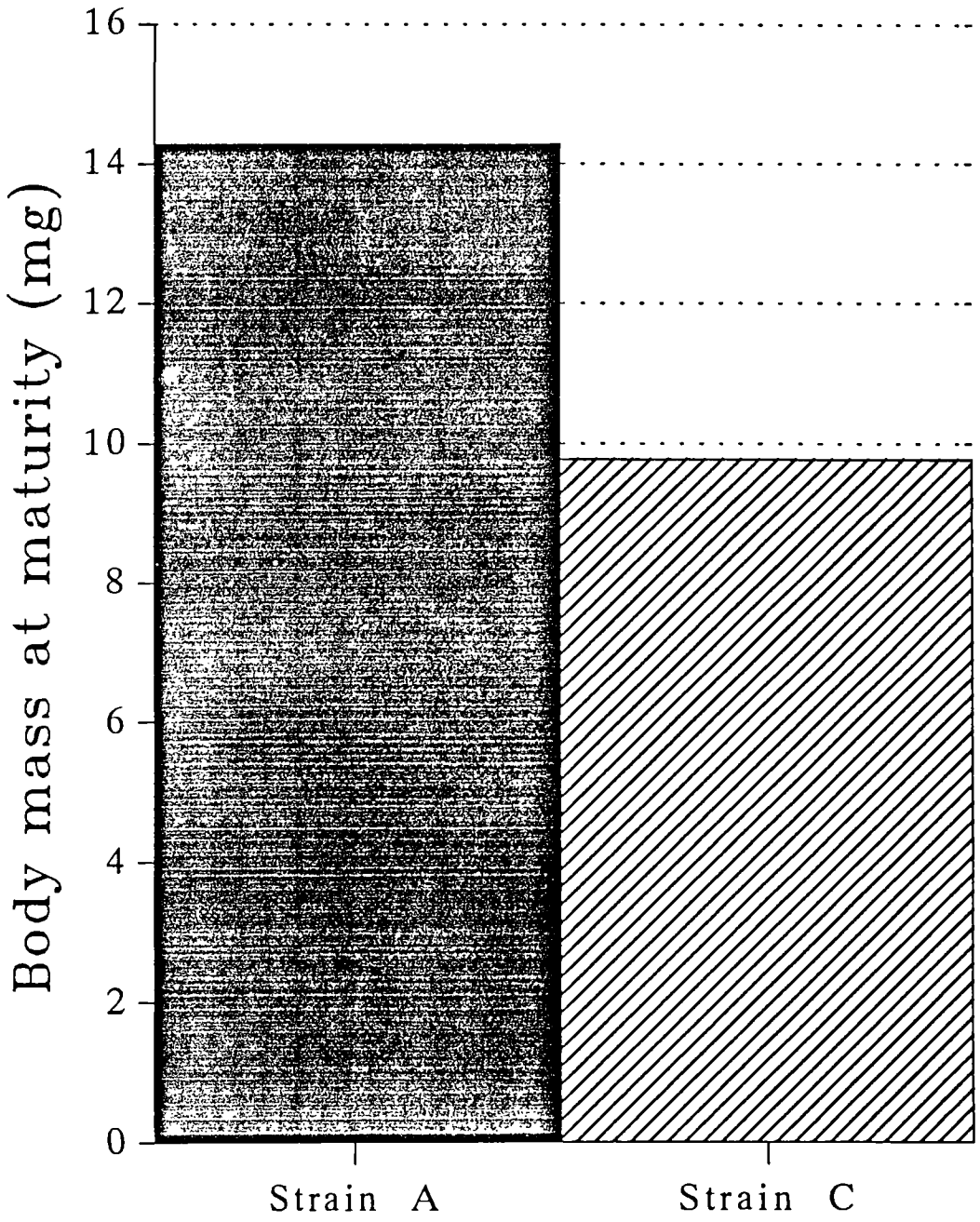

Figure 2.7: Body mass (in mg) of strain A and C atthe size of maturity when reared under constant laboratory conditions Body mass was predicted from length weight curves of strains A and C. Graph showsstrain C mature at a smaller size.

The life tables produced from survivorship analysis (see Appendix 2) allowed Ro (net rate of population increase) to be calculated for the two strains. The standard calculation of Ro requires all the snails to have died by the end of the experiment. This investigation ceased after 54 weeks and some of the snails were still living. The Ro values calculated are based on survivorship upto the end of the experiment.

Ro is given by the equation:

$$Ro=\sum l_x m_x$$

where l_x= survivorship at time x

and m_x= fecundity at time x.

$$Ro_{\text{strain A}}=25.46 \quad Ro_{\text{strain C}}=42.03$$

The Ro values demonstrate that during the time of the investigation the reproductive effort of strain C was greater than that of strain A.

2.33 Length-Weight Curves

Length-weight curves produced for strain A and C are shown in Figures 2.8-2.11. A linear regression analysis performed showed a proportional relationship between length and weight. The regression equations for the two strains are:

STRAIN A $y= 3.28 + 2.36x$

STRAIN C $y= -2.25 + 2.85x$ where, y= log weight x= log length.

Significance tests for variation of body mass and regression coefficents are shown in Tables 2.7ab and 2.8ab.

The t-test performed on strain A and C showed them both to have highly significant positive regression (Tables 2.7a and 2.8a respectively). Both strains also have highly significant F values, hence a large proportion of the variance of body mass is explained by the regression on shell length (Tables 2.7b and 2.8b).

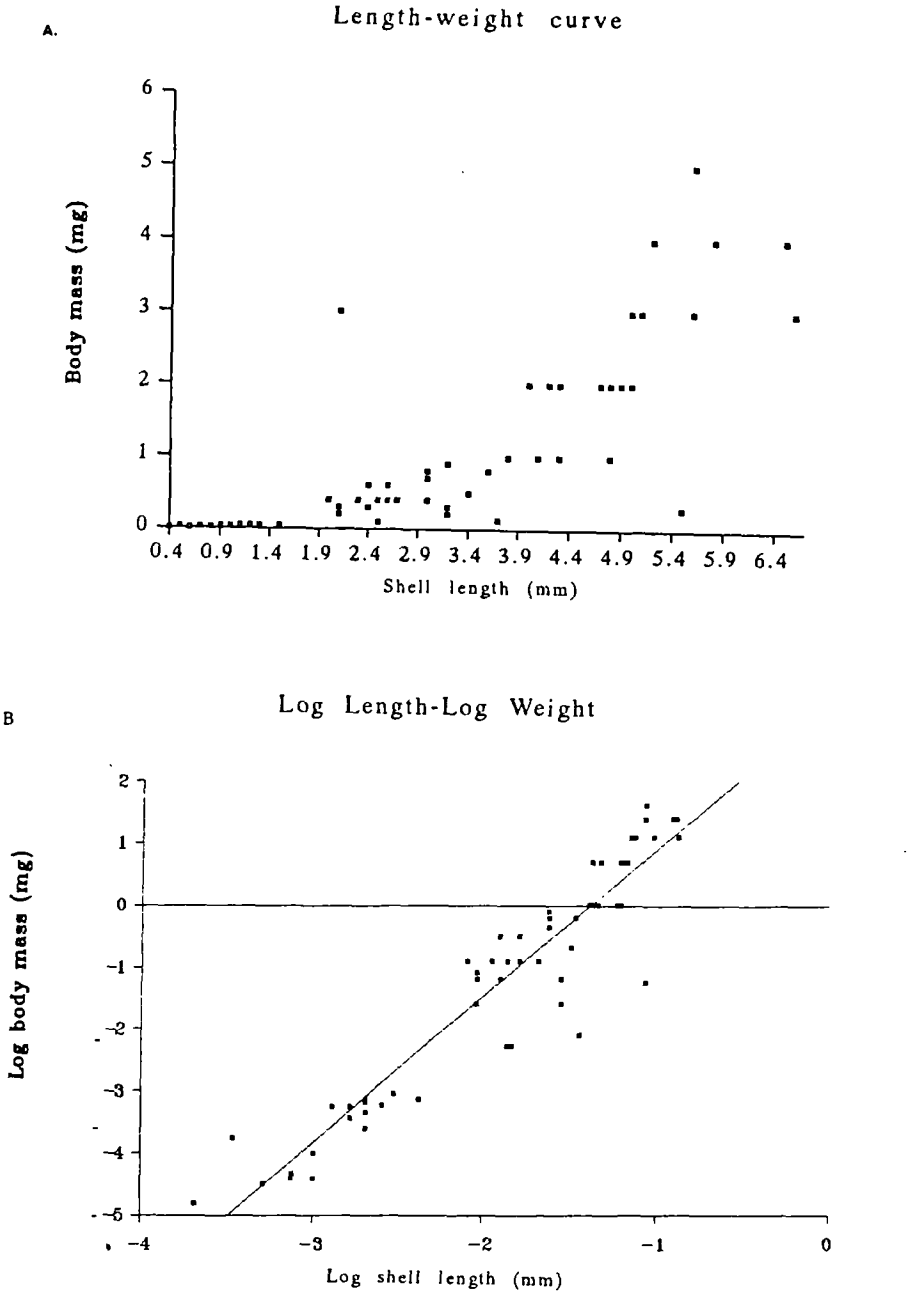

Figure 2.8: The relationship between shell free, tissue dry weight and shell length in strain A. (A) length-weight curve and (B) log transformed data.

Table 2.7A: A t-test is used to test of significance of regression coefficient and intercept for the length weight curves of strain A. The test was performed on MINITAB.

Predictor	Coefficient	Stdev.	t-ratio	P
Intercept	3.28	0.24	13.74	0.000
Slope	2.36	0.12	19.64	0.000

$r^2 = 86.0\%$ $r^2_{adj} = 85.7\%$

Table 2.7B: ANOVA (MINITAB) performed to measure the amount of linear variation in body mass is accounted for by the variation on shell length (mm) in strain A.

SOURCE	SS	MS	D.F	F	P
REGRESSION	183.41	183.41	1	385.87	0.002
ERROR	29.94	148	63		
TOTAL	213.36		64		

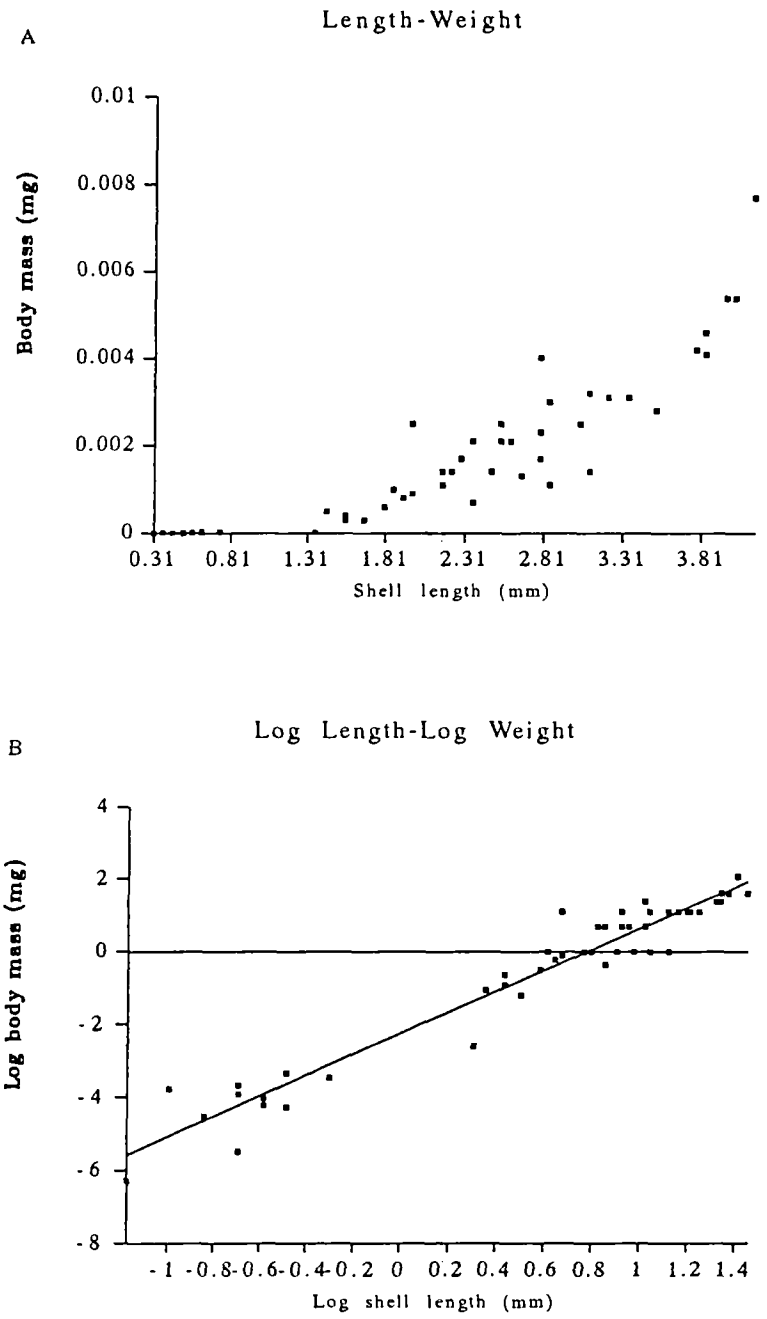

Figure 2.9: Relationship between shell free, tissue dry weight and shell length in strain C. (A) Length-weight curve and (B) log transformed data.

Table 2.8A: A t-test is used to test of significance of regression coefficient and intercept for the length weight curves of strain C. The test was performed on MINITAB.

Predictor	Coefficient	Stdev.	t-ratio	P
Intercept	-2.25	0.093	-24.30	0.000
Slope	2.86	0.099	28.66	0.000

$r^2 = 94.5\%$ $r^2_{adj} = 94.4\%$

Table 2.8B: ANOVA (MINITAB) performed to measure the amount of linear variation in body mass is accounted for by the variation on shell length (mm) in strain C.

SOURCE	SS	MS	D.F	F	P
REGRESSION	231.53	231.53	1	821.36	0.000
ERROR	13.53	0.28	48		
TOTAL	245.06		49		

2.4 DISCUSSION

The two strains of *Potamopyrgus jenkinsi* showed statistically significant differences in life-history parameters. Strain A had a longer juvenile period, and only showed accelerating growth after 20 weeks. By having a long juvenile period, strain A matured relatively late in its life and at a relatively large size (mean length when young first released = 4.66mm, S.E=0.29 as opposed to 4.22mm S.E=0.57 in strain C). Consequently, strain A released fewer young per adult lifetime. In contrast, strain C showed rapid growth in the first 20 weeks and by week 22 was already releasing young. This earliness in maturation was compensated by decelerating growth and smaller final size. Thus strain C snails showed greater reproductive effort in releasing many young early in adult life, but in doing so traded-off growth for reproduction.

Trade-offs between reproduction and somatic investment are predicted by life-history theory (Gadgil and Bossert, 1970; Pianka and Parker, 1975; Stearns, 1976; Tuomi *et al.*, 1983) and, indeed, investment per offspring empirically has been shown to occur at the expense of somatic investment (e.g. Etter, 1989; Green and Rothstein, 1991), with those individuals within a species having the smaller adult size also having the highest reproductive effort. Thus, the cost of reproduction plays an important role in determining the relationship between growth and reproductive success.

The life span of *Potamopyrgus jenkinsi* in its natural environment is between 3-8 months (Winterbourn, 1970). However, in the present investigation individuals survived for up to 12 months. The mortality of strain A is greatest in the juvenile stage, but this is compensated by the large number of young released per individual. The high reproductive effort shown by strain C would be expected to be compensated by lower adult survivorship (Calow, 1979), but there seemed to be no such trade-off. Bell and Koufopanou (1986), however, stated that under optimal conditions such as might occur in laboratory cultures, there is no evidence that the measurement of phenotypic correlations reveals trade-offs. Thus the correlation between fecundity and survival frequently is zero.

The major differences in phenological properties between the two strains were growth, size at maturation and fecundity. The manifestation of these differences under uniform conditions suggests that they are genetically determined. This could be brought about by environmental selection pressure. As mentioned in the introduction, strain C snails are normally found in waters of a brackish nature. The snails used in this investigation were from a pond that is drained in winter. Because of the unpredictable conditions, selection favours early reproduction in size and age. This perhaps is because restriction in food supply limits the growth of the snails and necessitates reproduction at an earlier adult size. In an unpredictable environment, early reproduction clearly is advantageous and once begun, as much effort as possible should be invested into it. On the other hand, strain A is found in a more predictable environment, a freshwater stream. Thus it is to the advantage of the snails to adopt the greater lifetime fecundity made possible by a larger body size, even though this involves delayed maturation.

Whereas some workers have obtained similar results to those reported in this investigation (Calow, 1981; Brown *et al.*, 1985; Etter, 1989), others have not (Lam and Calow, 1990; Crowl, 1990). Thus, Lam and Calow (1990) reared two generations of snails in the laboratory. They found that by the second generation, differences between the two populations began to disappear. They suggested that there was a maternal effect on the offspring, which diminished among successive generations when cultures were maintained under carefully controlled constant laboratory conditions. However, although the phenotypic differences exhibited by the parent disappears, the common environmental effect may still prevail.

However, in the present case of strain A and C snails, the phenotypic differences probably can be explained at the level of the genotype. DNA fingerprinting of the three strains (A,B,C) of *P.jenkinsi* collected around Britain has shown them to posses consistently different genotypes, stable for at least two generations (Hauser *et al.*, 1992). Thus, the great experimental value of *P.jenkinsi* is that it is truly clonal. Any genetic

changes that take place are through mutation. While environmental factors explain most variation in life histories, genetic differences are important and need to be considered. The marked genetic differences between strains A, B and C (Johnson, 1981; Hauser *et al.*, 1992) undoubtedly arose before these clones were introduced to Britain and probably reflect independent origins from sexual ancestors in New Zealand.

The life-history characteristics of the two strains differed significantly and, in view of the fingerprinting studies, are probably genetically determined. Exactly how plastic these phenotypes are under manipulated environmental conditions is considered in the following chapters.

CHAPTER 3:

THE RESPONSE IN LIFE HISTORY TO FOOD STRESS

SUMMARY

The effects of starvation and food ration on the growth, survivorship and fecundity of the two strains A and C of *Potamopyrgus jenkinsi* were measured. Food shortage reduced the growth rate and survivorship of the two strains. Reproduction in strain A ceased when starved, whereas strain C continued to release young, though the numbers were reduced. Both strains, therefore, were plastic in their growth and reproductive traits, but showed different responsiveness to food availability.

3.1 INTRODUCTION

Because growth and reproduction make competing demands on a limited energy budget, individuals that invest energy into reproduction early in their life history may grow only to a relatively small size. If fecundity is proportional to maternal size, these early-maturing individuals may have a reduced lifetime reproductive output. Conversely, individuals that direct energy to growth in the early stages of their life-history, so growing larger and reproducing later, may be capable of producing more young during their lives (Spight and Emlen, 1976).

Strategies of energy allocation, however, may change according to food availability, so affecting growth and even fecundity. Thus predictions of life-history theory using characteristics based on growth rates may not be straightforward (Stearns and Koella, 1986). For example, three models for energy allocation in *Daphnia* have been proposed by Kooijman (1986), McCauley *et al.* (1990) and Bradley *et al.*(1991). All three give priority to somatic maintenance over reproduction, which in turn has priority over growth. It is predicted, therefore, that individuals which are subjected to increasingly limited food supply, cease growth first, then reproduction, followed by death. In an experimental study of the effect of food limitation on energy allocation in *Daphnia*, Bradley *et al.* (1991) found that reproduction ceased whereas growth did not. Thus, in *Daphnia* maintenance has priority over growth, which in turn has priority over reproduction.

It is possible that priorities of energy allocation vary adaptively among species, or even among populations within species. Thus food deprivation may lead some individuals to cease reproduction to ensure their survival, while others may show a 'high suicidal' rate of reproduction (Reznick, 1985). Calow and Woolhead (1977) demonstrated such a cost of reproduction in triclads, reproductive individuals having shorter life spans than non-reproducers.

Experimental manipulation of the life history through food ration can reveal how a given genotype will respond to changes in the environment. This technique is especially powerful if genotypes can be replicated, as in clonal organisms, enabling each genotype to be exposed to all experimental treatments. Keen and Gong (1989), working on the clonal cnidarian *Aurelia aurita* found that with frequent food supply some individuals grew rapidly, while others were unable to utilise the extra food. This suggests that the relative success of different genotypes (clones) may have a strong environmental component (Hoffman, 1986). A significant amount of variation in clonal growth can be explained by environmental change. However, it is the genotype which influences the growth. These factors in turn influence the clones' survivorship and investment into sexual reproduction.

To investigate genotype-environment interactions involving energy allocation to growth, reproduction and survival the two strains A and C of *Potamopyrgus jenkinsi* were compared. As mentioned in the General Introduction a genotype may produce a range of phenotypes in various environmental conditions. This phenotypic plasticity may be expressed numerically as a reaction norm (Woltereck;1909, cited from Stearns;1989b).

Growth and developmental rates are often phenotypically plastic (Stearns and Koella, 1986). For example, Newman (1989), found that tadpoles of *Scaphopus couchii* metamorphose earlier in small ephemeral ponds than in larger, permanent ponds.

Phenotypic plasticity, however, does not necessarily mean that the genotype will perform equally well in all environments. Resources are in fact allocated such that the optimal life history is achieved for a particular environment within the set of possible environments. Nevertheless, a genotype adapted to a range of environments will generally outcompete genotypes that produce a single phenotype highly adapted to only one of those environments (Stearns *et al.*, 1991).

The following investigation is divided into two parts, investigating the effect of (a) starvation and (b) level of food supply on the life history parameters mentioned above.

Particular interest is paid to the effect of these factors on fecundity, especially in the second experiment, in order to determine whether there is a threshold level of food supply required for the production and release of young, or whether individuals show a 'suicidal' rate of reproduction when in negative energy balance. If the two strains show different plasticity in response to food supply, this must reflect a clonal and therefore genotypic effect.

3.2 MATERIALS AND METHOD

3.21 EXPERIMENT 1: STARVATION

The two strains A and C were divided into three size classes: newly released juveniles (0-0.61mm), large juveniles (0.62-1.86mm) and adults (1.87-3.04mm). Individuals from each size class were either deprived of food (starved) or fed. In either regime, four replicate pots contained 10 snails (total sample size = 40). Every seven days over a period of 21 weeks growth, mortality and fecundity were measured and recorded as described in 1.83 General Methods (chapter 1).

3.22 EXPERIMENT 2: FOOD RATION

The two strains A and C were divided into the same three size classes as described above. The snails were placed in four feeding treatments: high ration (continuously fed), medium ration (fed 3 days then starved 4 days), low ration (fed one day then starved 6 days) and continuously starved. As in the previous experiment, 4 replicate pots of 10 snails were used for each strain in each treatment. The experiment continued for 24 weeks. Measurements of growth, mortality and fecundity were taken every fourteen days.

3.3 STATISTICAL ANALYSIS

3.31 Growth

A univariate, repeated measures, nested MANOVA (SPSS) was used to examine the effect of environment and strain on growth rate and final mean shell length (mm). The MANOVA repeated measures design, as obtained in a time series, has the added advantage that it does not assume the growth to be linear. A univariate design was used here and in chapter 4 because the sample sizes were unequal due to snails dying during the investigation. Because of the nested design two error terms appear (see result tables in sections 3.4). The first (ERROR) refers to the individual variation of the snails, growth and size, the second (ERROR1) refers to the error between the pots.

3.32 Survivorship

The effect of the environment on the two strains was examined using survivorship analysis (SPSS) as described in chapter 2. First generated is an overall comparison of the survivorship of the two strains in the various environments. Pairwise comparisons are then made between each strain and treatment, using the Lee-Desu statistic (Lee and Desu, 1972).

3.33 Fecundity

The effect of environment on the total release of young in the two strains was tested with ANOVA (MINITAB). In treatments where both strains released young, a two-way ANOVA was used for comparisons between strains and among treatments. Additionally, a one-way ANOVA was applied to the data for strain C, which released young in all treatments.

3.4 RESULTS

3.41 EXPERIMENT I: STARVATION

3.411 Growth

Growth curves for the three size classes are shown in Figures 3.1-3.3. In all size classes the snails present in the starved regime showed less growth and attained a smaller size than those that were fed. This result is confirmed by MANOVA (Tables 3.1-3.3), which showed the differences between the treatments to be significant.

Although the fed and starved environment was shown to significantly affect the final size of the snails, a significant difference between strains was demonstrated in only the large juvenile size class (MANOVA, $F_{1,12}$=37.35, P=0.00). Strain C fed and starved snails showing greater growth than strain A. As demonstrated in chapter 2, strain C shows its greatest growth at this stage of its life history (Figure 2.1) and this may explain the significant difference observed. However, in all three size classes the growth rates (STRAIN x TIME interaction) of the strains differed significantly (Tables 3.1-3.3). In fact, highly significant results were found for all the time effects. This is to be expected, as initially the snails will react in the same way and then as time goes on they will gradually diverge.

The two strains were shown to be plastic in their response to the environment. Significant interactions of STRAIN x TREATMENT and STRAIN x TREATMENT x TIME in the large juvenile and adult size classes (Tables 3.2 and 3.3), demonstrated differences among the treatments, but the nature of the differences varied between the two strains.

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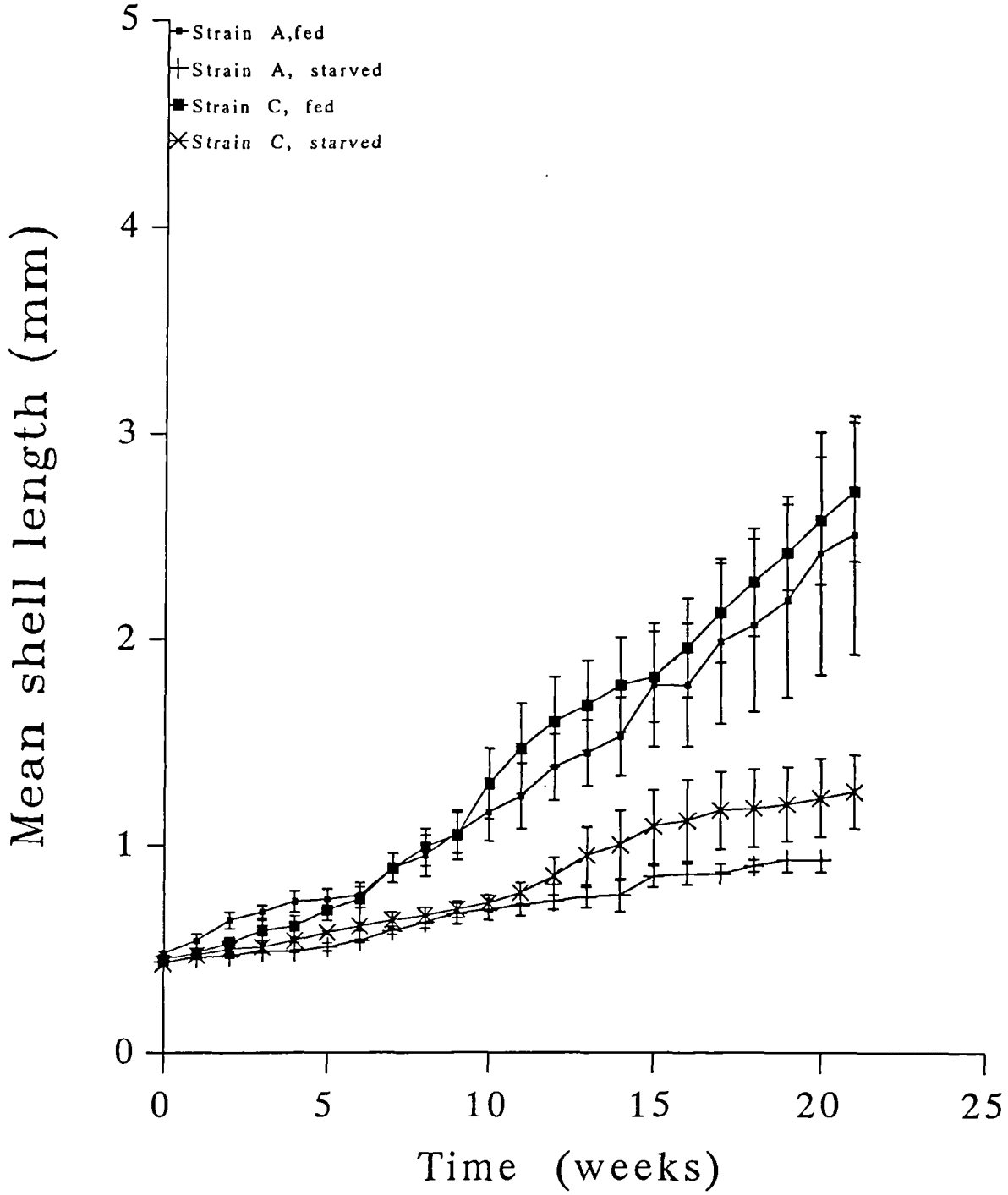


Figure 3.1: Growth of strain A and C newly released juveniles in fed and starved environments. Points are means, vertical lines standard error bars.

:size class: 0.62-1.86mm

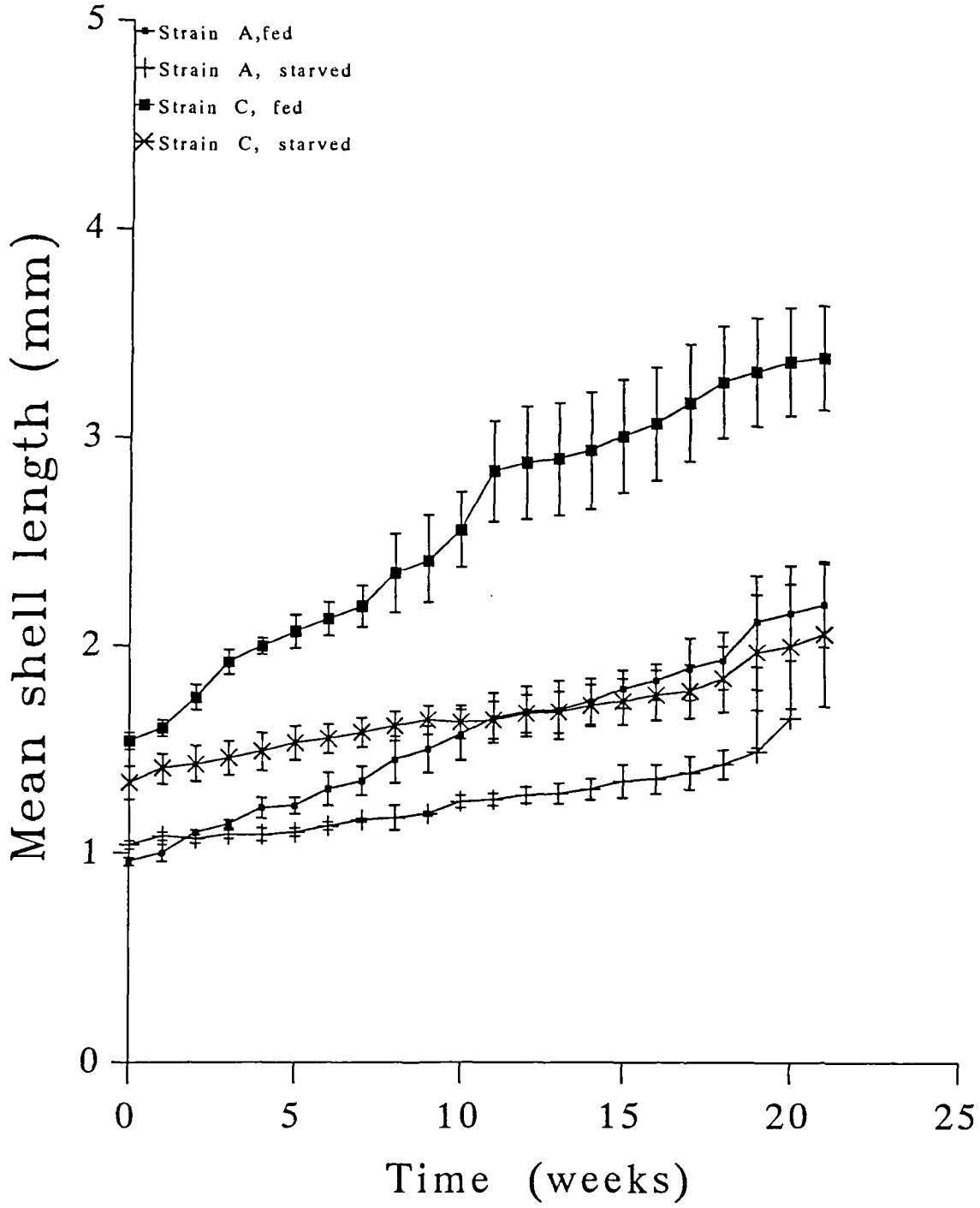
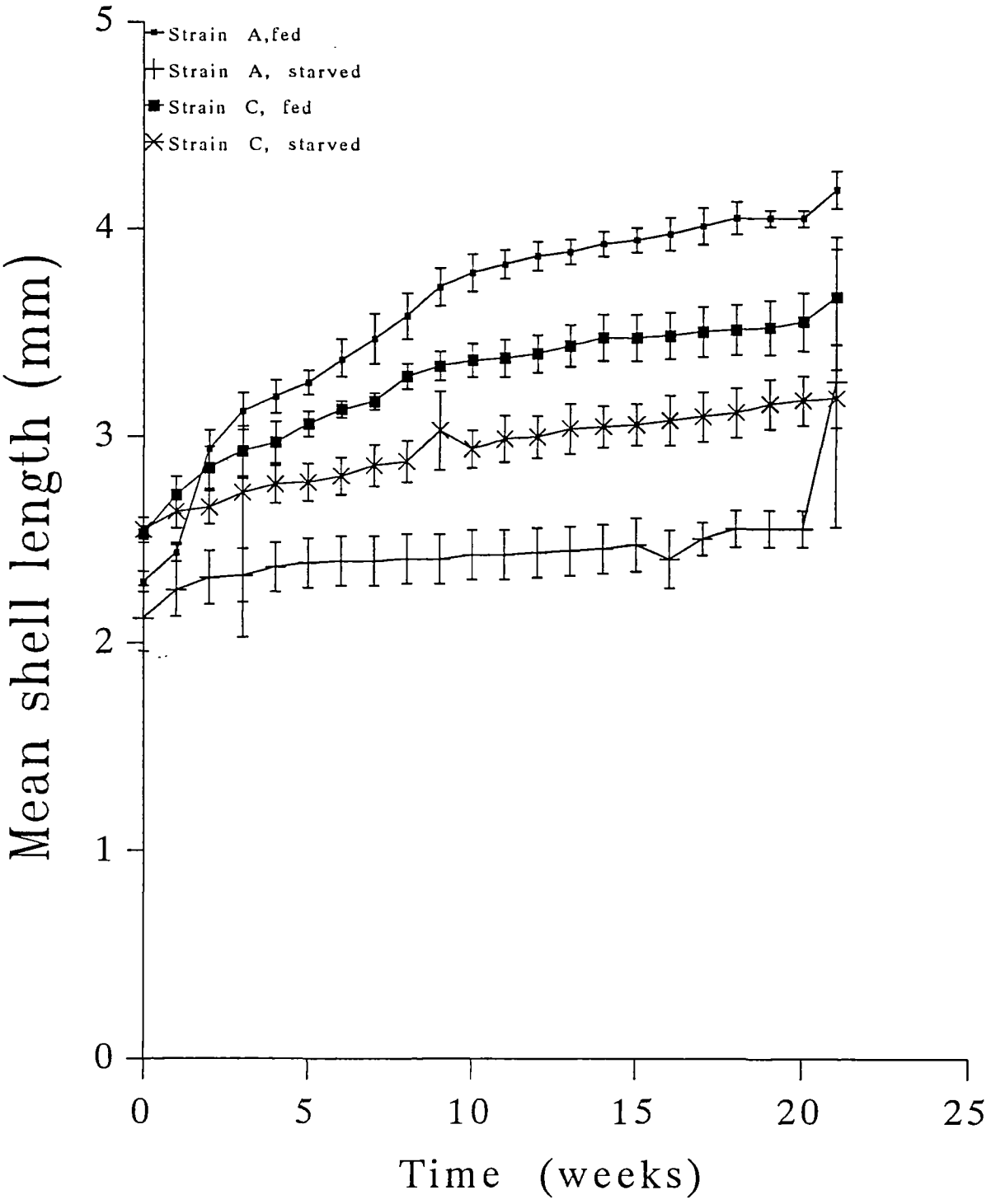


Figure 3.2: Growth of strain A and C large juveniles in fed and starved environments. Points are means, vertical lines represent standard error bars

size class: 1.87-3.04mm



ure 3.3: Growth of strain A and C adults in fed and starved environments. Points are means, vertical lines represent standard error bars.

Table 3.1: Nested MANOVA (SPSS) on the effect of fed and starved environments on growth and overall mean shell length (mm) in newly released juvenile strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	0.85	1	0.85	0.89	0.365
TREAT	19.83	1	19.83	20.57	0.001
STRAIN BY TREAT	0.03	1	0.03	0.03	0.856
ERROR 1	11.57	12	0.96		
TIME	41.62	5	8.32	600.54	0.000
TIME BY STRAIN	0.90	5	0.18	12.93	0.000
TIME BY TREAT	10.65	5	2.13	153.63	0.000
STRAIN BY TREAT BY TIME	0.12	5	0.02	1.68	0.140
ERROR	3.11	224	0.01		

Table 3.2: Nested MANOVA (SPSS) on the effect of fed and starved environments on growth and overall mean shell length (mm) in large juvenile A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	28.83	1	28.83	37.23	0.000
TREAT	23.30	1	23.30	30.08	0.000
STRAIN BY TREAT	5.58	1	5.58	7.21	0.020
ERROR 1	9.29	12	0.77		
TIME	30.86	5	6.17	634.69	0.000
TIME BY STRAIN	1.26	5	0.25	25.85	0.000
TIME BY TREAT	7.10	5	1.42	146.00	0.000
STRAIN BY TREAT BY TIME	0.86	5	0.17	17.69	0.000
ERROR	2.28	234	0.01		

Table 3.3: Nested MANOVA (SPSS) on the effect of fed and starved environments on growth and overall mean shell length (mm) in adult strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	0.15	1	0.15	0.21	0.657
TREAT	35.81	1	35.81	50.15	0.000
STRAIN BY TREAT	10.38	1	10.38	14.53	0.002
ERROR 1	8.57	12	0.71		
TIME	24.32	5	4.86	295.35	0.000
TIME BY STRAIN	0.72	5	0.14	8.72	0.000
TIME BY TREAT	4.92	5	0.98	59.80	0.000
STRAIN BY TREAT BY TIME	1.55	5	0.31	18.79	0.000
ERROR	4.03	245	0.02		

3.412 Survivorship

When starved, the survivorship of newly released juveniles decreased sharply (Figure 3.4). The overall comparison test demonstrated this decrease to be significant (D-statistic= 13.94, D.F.= 1, P= 0.0002). A significant difference was also found between the two strains, strain C demonstrating the greater survivorship in either treatment (D-statistic= 6.2, D.F.=1, P= 0.013). Pairwise comparison tests (Table 3.4B) showed strain A and C to have similar survivorship when starved. However, significant differences were found when fed strain C snails were compared to strain A snails in either treatment (Table 3.4B). In all cases fed strain C showed the greater survivorship (see appendix 2.21 for median life span).

As is clearly demonstrated in Figure 3.5, the survivorship pattern of fed and starved snails did not differ significantly (D-statistic= 0.88, D.F.= 1, P= 0.35) in the large juvenile size class. However, a small but significant difference was found when the strains were compared (D-statistic= 4.08, D.F.= 1, P= 0.043). Unlike the previous size class, strain A showed greater survivorship in either regime. At this stage of the snail's life history, the growth of strain C is greater than that of strain A. Thus a possible trade-off between growth and survivorship may be taking place. Pairwise comparison tests (Table 3.5B) also showed the survivorship of the strains not to depend on their feeding environment.

The survivorship of the adult snails was significantly reduced in the starved environment as shown in Figure 3.6 (D-statistic= 10.79, D.F= 1, P= 0.001). A significant found was also found between the two strains, strain C showing the greater survivorship (Figure 3.6, Table 3.6A).

As demonstrated in Figure 3.6 and confirmed by the pairwise comparison tests, the survivorship of strain C fed snails was significantly greater than strain C starved snails (D-statistic= 14.41, D.F.= 1, P<0.001). However, the survivorship of strain A fed and starved snails was similar. Such a result can be explained by the different reproductive tactics adopted by the two strains when starved (See section 3.413).

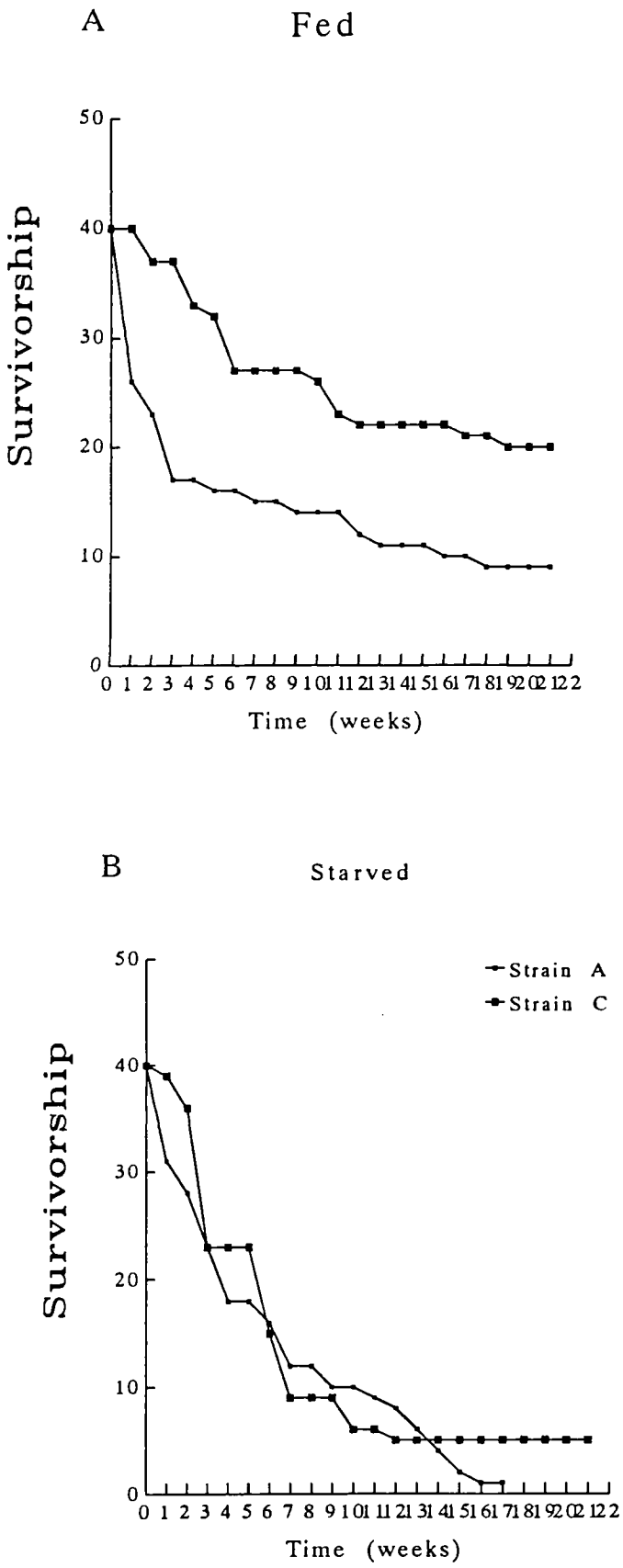


Figure 3.4: Survivorship of newly released juveniles when (A) Fed and (B) starved.

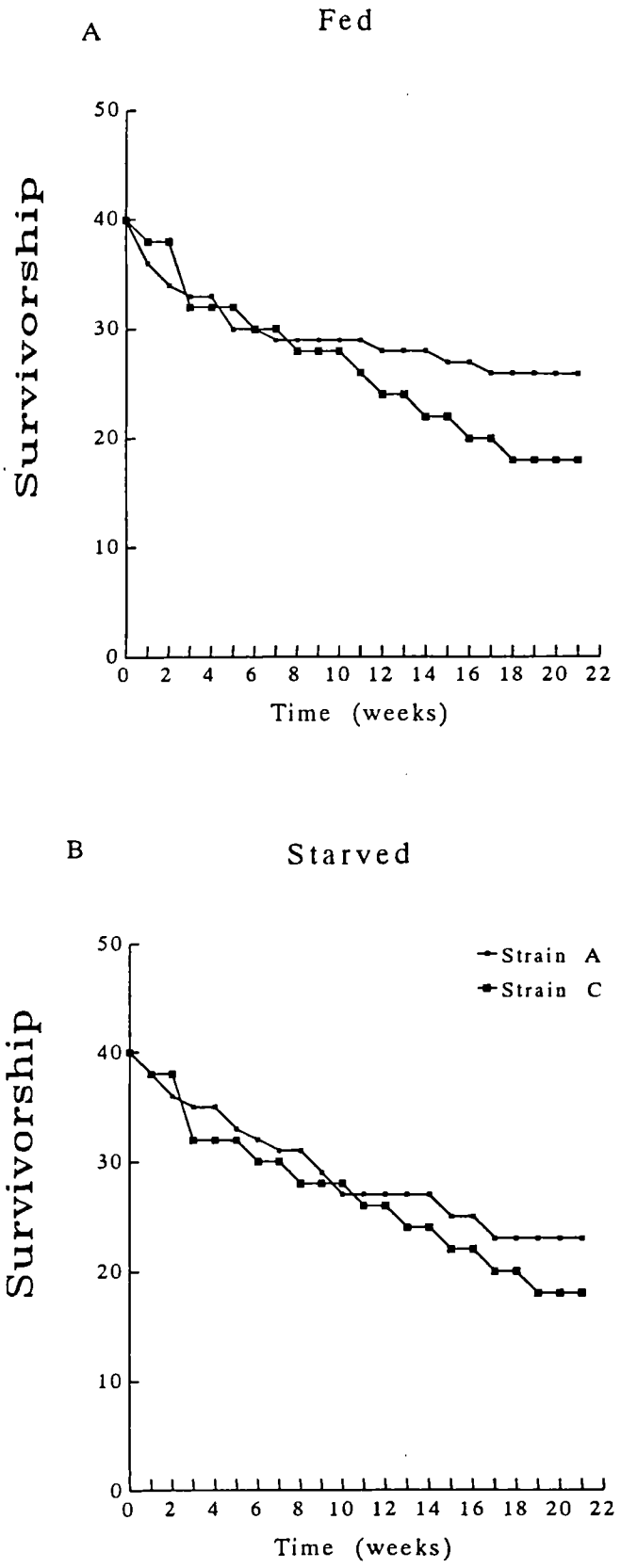


Figure 3.5: Survivorship in large juveniles in (A) fed and (B) starved regimes.

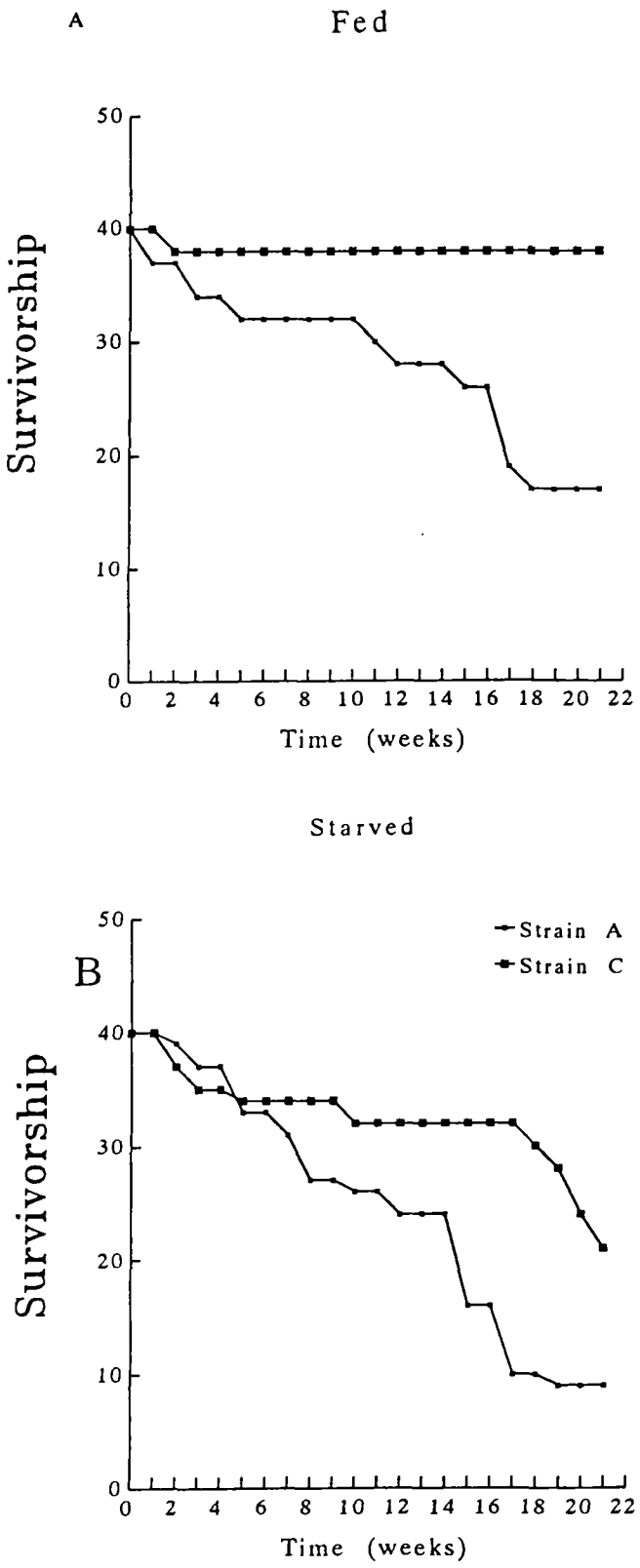


Figure 3.6: Survivorship of adults in (A) fed and (B) starved environments for the period of 21 weeks.

Table 3.4: Survivorship analysis using Lee-Desu Statistic (D) for (A) Overall and (B) Pairwise Comparison of the survival between the strains when fed and starved in newly released juveniles. (*P=0.01-0.05, **P=0.005-0.01, ***P= < 0.005 NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	6.209	1	0.0127
Fed vs Starved	13.938	1	0.0002

B. Pairwise Comparison

Comparison	Strain C Starved	Strain C Fed	Strain A Starved	Strain A Fed
Strain A Fed	NS	14.44 **	NS	---
Strain A Starved	NS	21.68**	---	
Strain C Fed	14.4***	---		
Strain C Starved	---			

Table 3.5: Survivorship analysis using Lee-Desu Statistic (D) for A) Overall and B) Pairwise Comparison of the survival between the strains when fed and starved in large juveniles. (*P=0.01-0.05, **P=0.005-0.01, ***P= < 0.005, NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	4.082	1	0.0433
Fed vs Starved	0.875	1	0.3495

B. Pairwise Comparison

Comparison	Strain C Starved	Strain C Fed	Strain A Starved	Strain A Fed
Strain A Fed	NS	NS	NS	---
Strain A Starved	NS	NS	---	
Strain C Fed	NS	---		
Strain C Starved	---			

Table 3.6: Survivorship analysis using Lee-Desu Statistic (D) for Overall (A) and Pairwise Comparison (B) of the survival between the strains when fed and starved in adult.(*P=0.01-0.05, **P=0.005-0.01, ***P= < 0.005, NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	27.952	1	0.000
Fed vs Starved	10.792	1	0.001

B. Pairwise Comparison

Comparison	Strain C Starved	Strain C Fed	Strain A Starved	Strain A Fed
Strain A Fed	NS	22.302**	NS	---
Strain A Starved	NS	35.207**	---	
Strain C Fed	14.41**	---		
Strain C Starved	---			

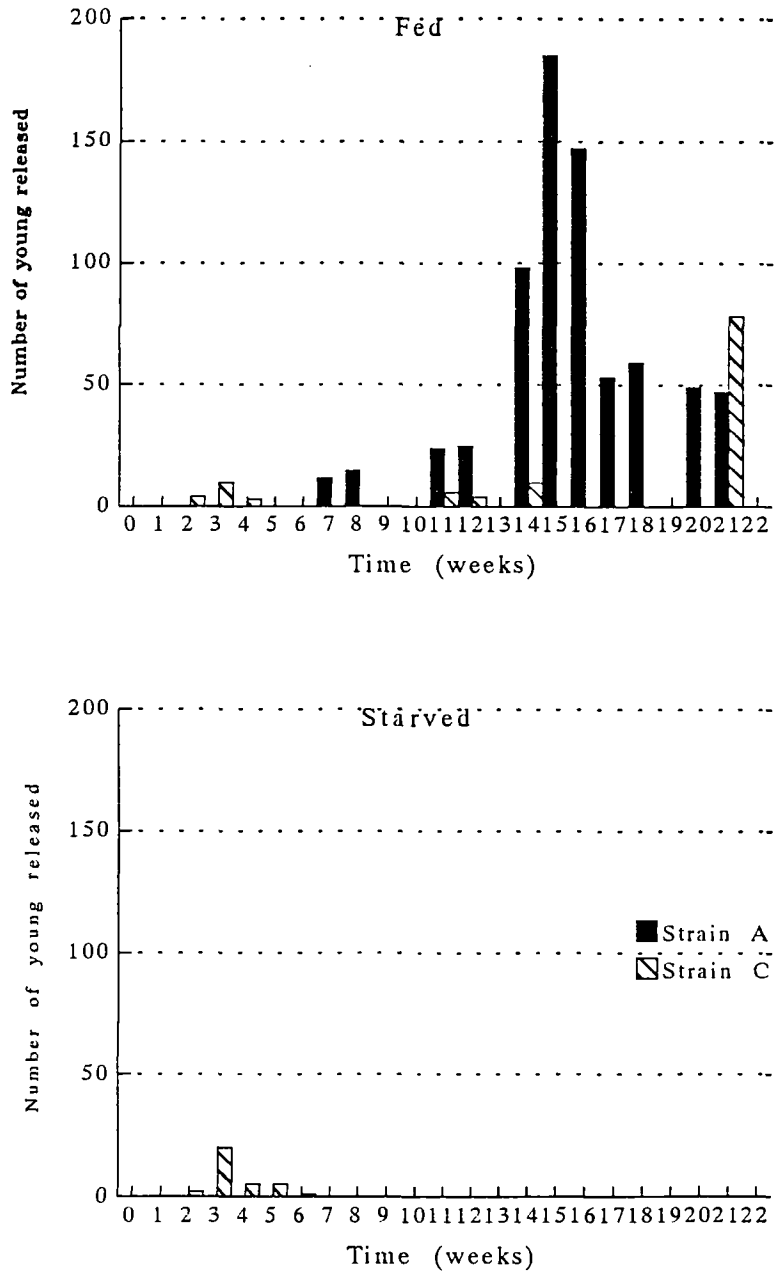


Figure 3.7: Weekly reproductive output of strain A and C adults when fed and starved. Strain C released young in both feeding regimes, strain A when fed.

Table 3.7a: ANOVA of the total fecundity between strain A and C snails when fed.

SOURCE	SS	MS	D.F.	F	P
STRAIN	42021	42021	1	9.09	0.011
ERROR	55480	4623	12		
TOTAL	97500		13		

Table 3.7b: ANOVA of the total fecundity of strain C snails in fed and starved regimes.

SOURCE	SS	MS	D.F.	F	P
TREAT	1208	1208	1	5.76	0.031
ERROR	2935	2935	14		
TOTAL	4142		15		

3.413 Fecundity

Reproductive activity was shown only in the adult size class. Strain C snails released young in both the fed and starved regimes (Figure 3.7). Strain A only released young in the fed treatment and did so six weeks after fed strain C snails (Figure 3.7). The total number expelled each week by strain A was greater than the number released by strain C. ANOVA (Table 3.7a) showed strain A to have a significantly greater reproductive output than strain C snails. Strain C released young in both treatments and the number of young released was significantly reduced when no food was present (Table 3.7b). The significant effect of treatment on the two strains causes them to alter their reproductive output differently in response to environmental conditions. Moreover, in the case of strain C continual release of young when starved was achieved at the cost of reduced survivorship (see section 3.412).

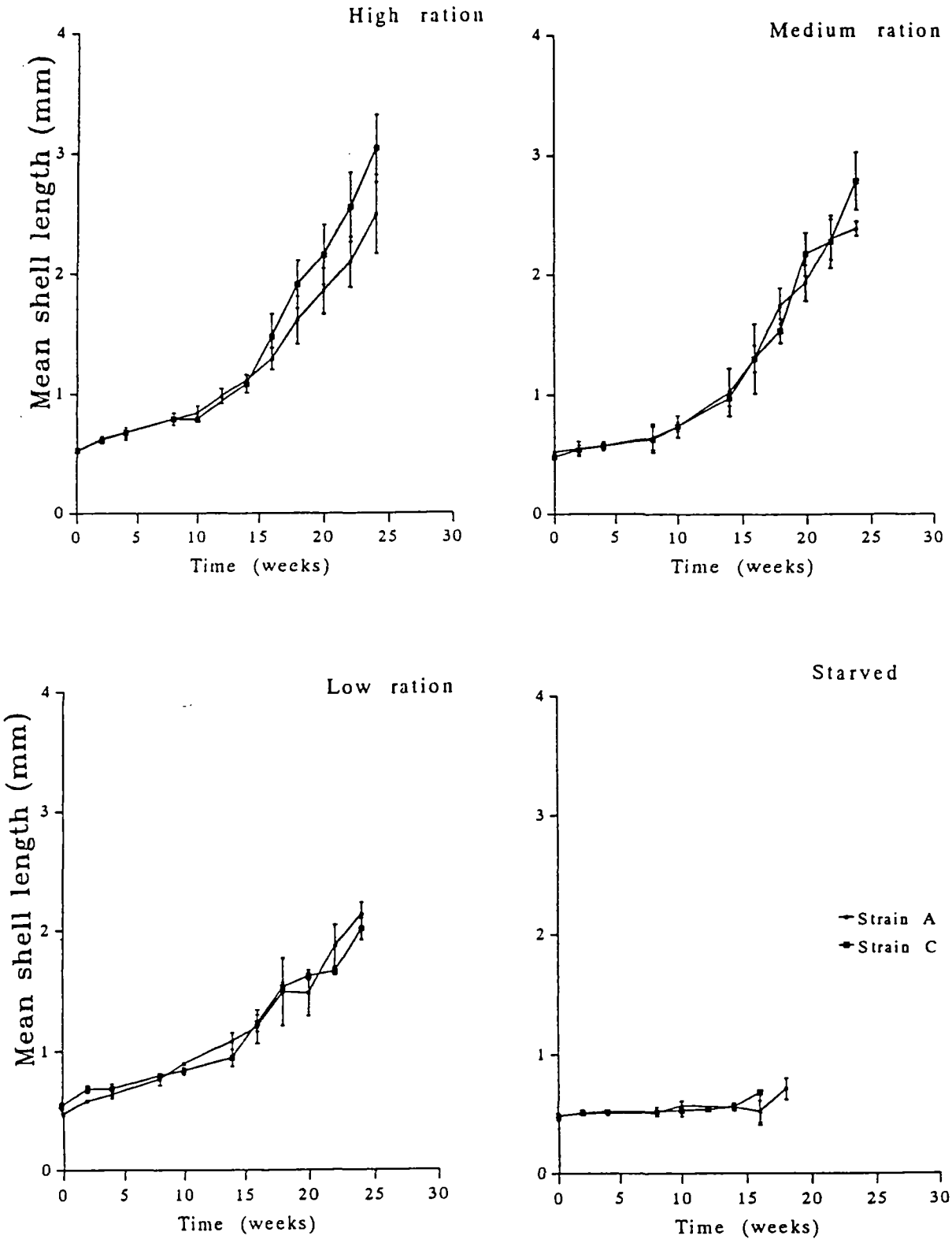
3.42 EXPERIMENT 2: FOOD RATION

3.421 Growth

Growth curves of the three size classes in the four feeding environments are shown in figures 3.8-3.10.

As in the starvation experiment strain A and C snails in the newly released juvenile and adult size classes did not show a significant difference in their final mean size (Tables 3.8 and 3.10). Only in the large juvenile size class did the strains differ significantly in size (Table 3.9). Unlike the starvation experiment, the growth rate of the strains was not significantly different in the two juvenile size classes (Tables 3.8-3.9). The adult snails of the two strains did differ significantly in growth rate (MANOVA, $F_{5,167}=3$, P=0.013).

The effect of the feeding environment on the snail's size was shown not to affect the newly released juveniles (Table 3.8), but in the two larger size classes treatment did affect the final size of the snails (Tables 3.9-3.10). Figures 3.9 and 3.10 show that different feeding regimes had a significant effect on the growth of the snails. Those in



Figur 3.8: Growth curves of strain Aand C newly released juveniles in varying food availability. Points are means, vertical lines error bars.

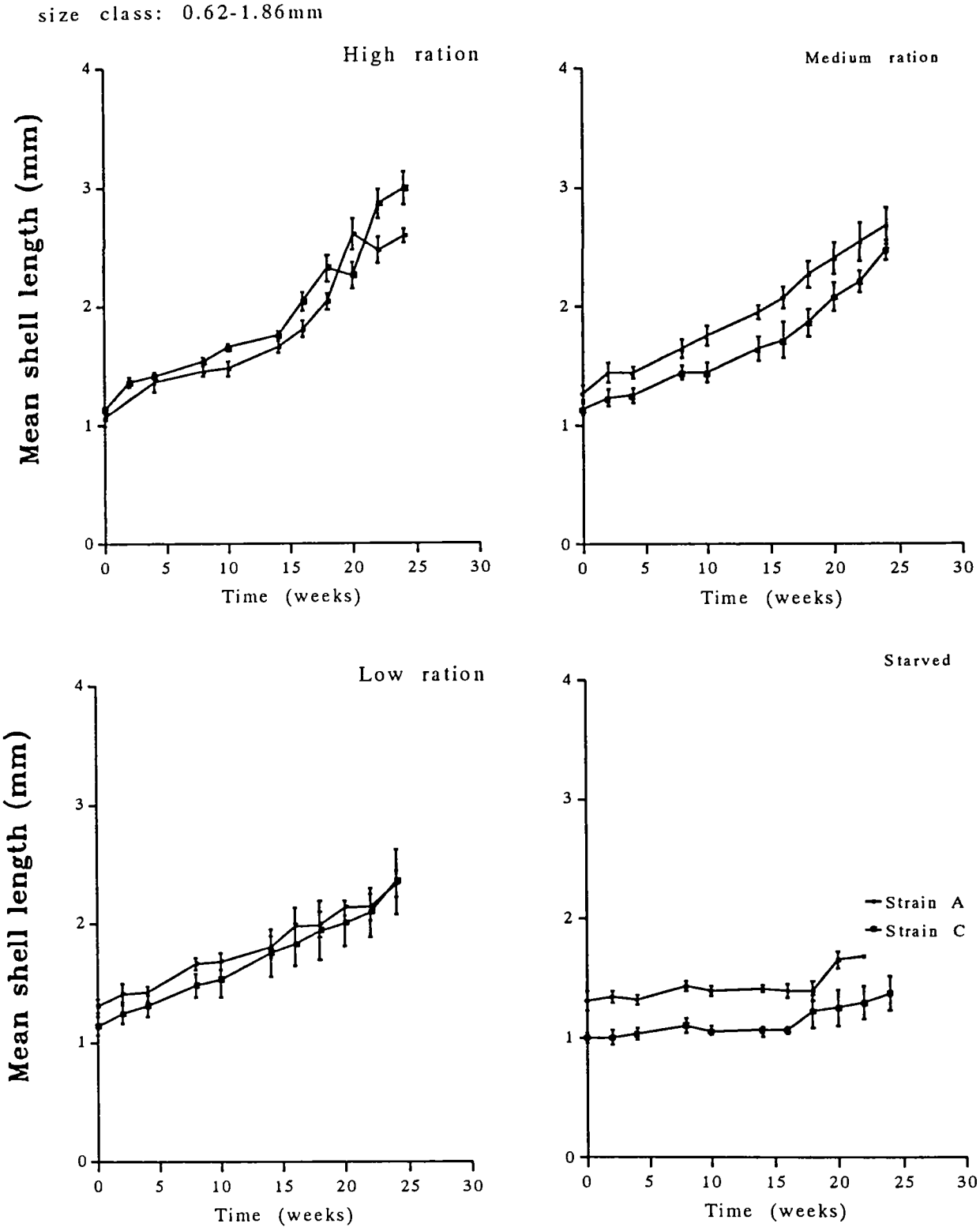


Figure 3.9: Growth curves of strain A and C large juvenile snails when present in 4 feeding regimes. Points are means, vertical lines error bars.

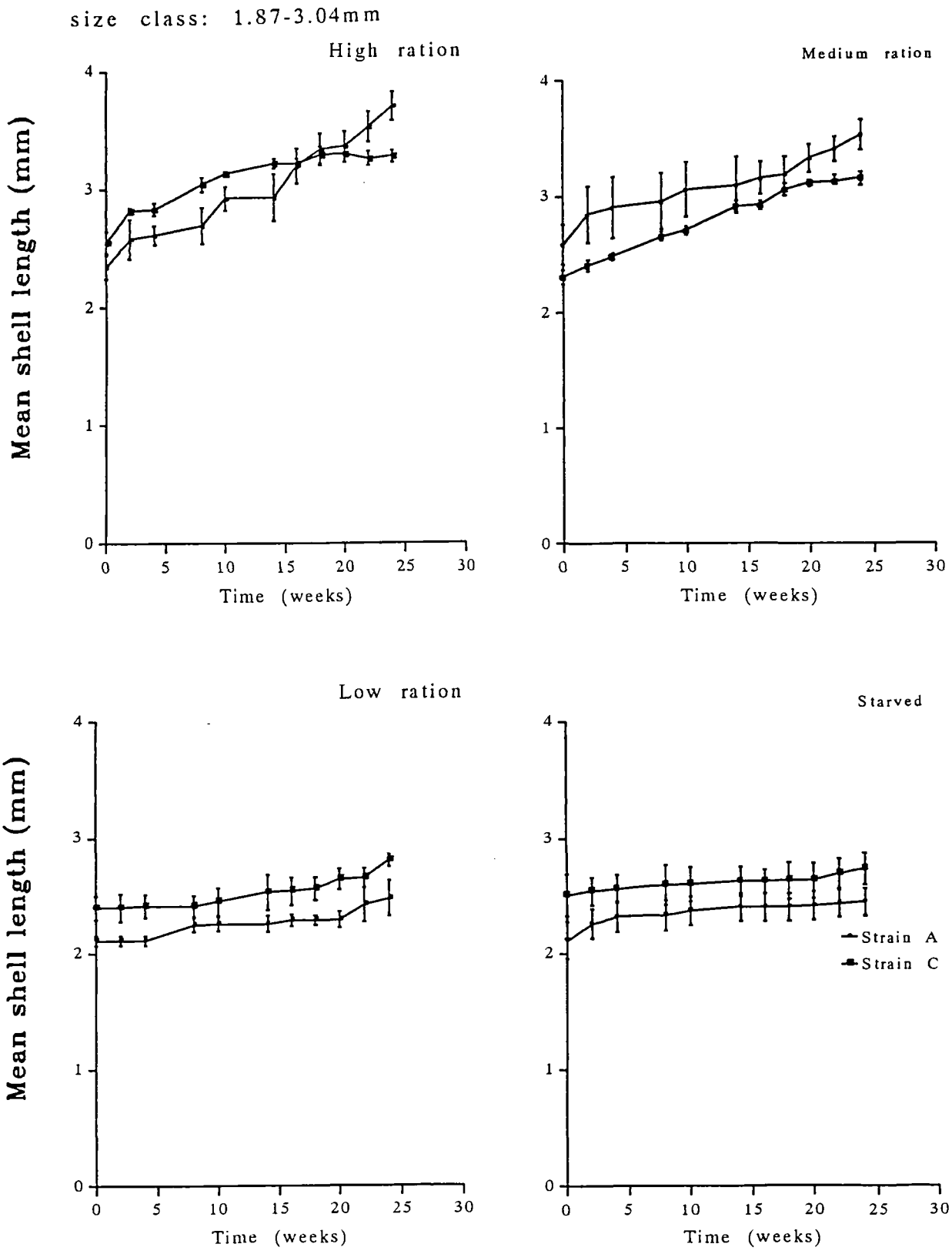


Figure 3.10: Growth in adult snails of strain A and C when placed in 4 feeding regimes. Points are means, vertical lines represent standard error bars.

Table 3.8: Nested MANOVA (SPSS) on the effect of varying food environments on growth and overall mean shell length (mm) in newly released juvenile strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	0.00	1	0.00	0.02	0.888
TREAT	1.27	3	0.42	2.16	0.119
STRAIN BY TREAT	0.20	3	0.07	0.34	0.797
ERROR 1	4.71	24	0.20		
TIME	15.03	5	3.01	50.38	0.000
TIME BY STRAIN	0.04	5	0.01	0.12	0.987
TIME BY TREAT	5.92	14	0.42	7.09	0.000
STRAIN BY TREAT BY TIME	0.76	14	0.05	0.91	0.548
ERROR	2.28	234	0.01		

Table 3.9: Nested MANOVA (SPSS) on the effect of varying food environments on growth and overall mean shel length (mm) in large juvenile strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	1.05	1	1.05	4.42	0.046
TREAT	10.43	3	3.48	14.59	0.000
STRAIN BY TREAT	2.70	3	0.90	3.78	0.024
ERROR 1	5.72	24	0.24		
TIME	35.20	5	7.04	192.41	0.000
TIME BY STRAIN	0.11	5	0.02	0.59	0.706
TIME BY TREAT	8.94	15	0.60	16.28	0.000
STRAIN BY TREAT BY TIME	0.51	15	0.03	0.92	0.541
ERROR	5.34	146	0.04		

Table 3.10: Nested MANOVA (SPSS) on the effect of varying food environments on growth and overall mean shell length (mm) in adult strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	0.27	1	0.27	0.60	0.448
TREAT	24.39	3	8.13	18.07	0.000
STRAIN BY TREAT	3.71	3	1.24	2.75	0.065
ERROR 1	10.80	24	0.45		
TIME	12.63	5	2.53	167.67	0.000
TIME BY STRAIN	0.23	5	0.05	3.00	0.013
TIME BY TREAT	4.58	15	0.31	20.28	0.000
STRAIN BY TREAT BY TIME	1.31	15	0.09	5.78	0.000
ERROR	2.52	167	0.02		

well fed environments showed greater growth than those on low ration and starved environments.

The two strains were shown to be plastic in their growth when placed in different environments. However they did not differ significantly in their degree of plasticity. Only the large juvenile size class with respect to the STRAIN x TREATMENT interaction (Table 3.9) and the adult size class with respect to the STRAIN x TREATMENT x TIME interaction (Table 3.10) showed differences in the degree of plasticity.

3.422 Survivorship

Decreasing food availability caused a significant reduction in survivorship of the snails in the newly released juvenile size class (Figure 3.11, D-statistic= 12.09, D.F.=3, P= 0.007). However, the survivorship of strain A and C was shown to be similar (Table 3.11A). Strain C survivorship was not affected by the feeding environment as the pairwise comparison tests confirm (Table 3.11B). A significant difference was found in the survivorship of strain A snails when those in low ration and starved environments were compared to those in high and medium ration (Table 3.11B). Pairwise comparison tests between the strains in all 4 treatments showed strain A to have the greater survivorship (Table 3.11B).

As in the previous size class, a reduction in food availability caused a significant reduction in survivorship of the large juvenile size class (D-statistic= 79.81, D.f.= 3, P<0.005). Although feeding environment was shown to affect the snail's survivorship (Figure 3.12, Table 3.12A) strain A and C did not differ in their survivorship. This is reflected in the pairwise comparison tests where strain A and C in each treatment showed similar survivorship (Table 3.12B).

The survivorship of adult snails was again significantly affected by the feeding environment (D-statistic= 13.17, D.F.= 3, P= 0.004). Those snails present in poor feeding conditions demonstrated lower survivorship than those in good feeding conditions (Figure 3.13). The exception was starved strain A snails, which suffered no deaths

size class: 0-0.61mm

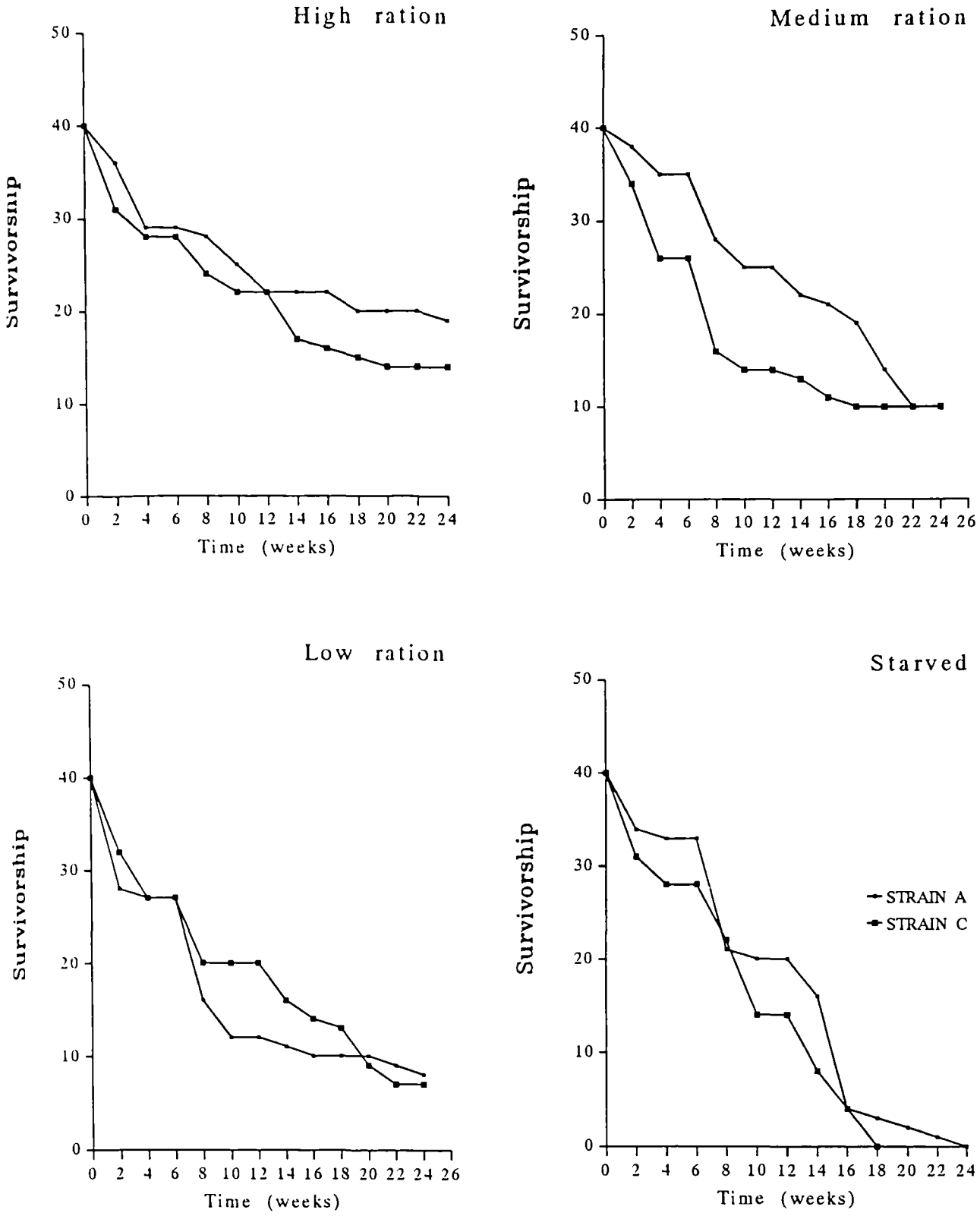


Figure 3.11: Survivorship curves of strain A and C newly released juveniles in the above 4 feeding regimes over a 24 week preiod.

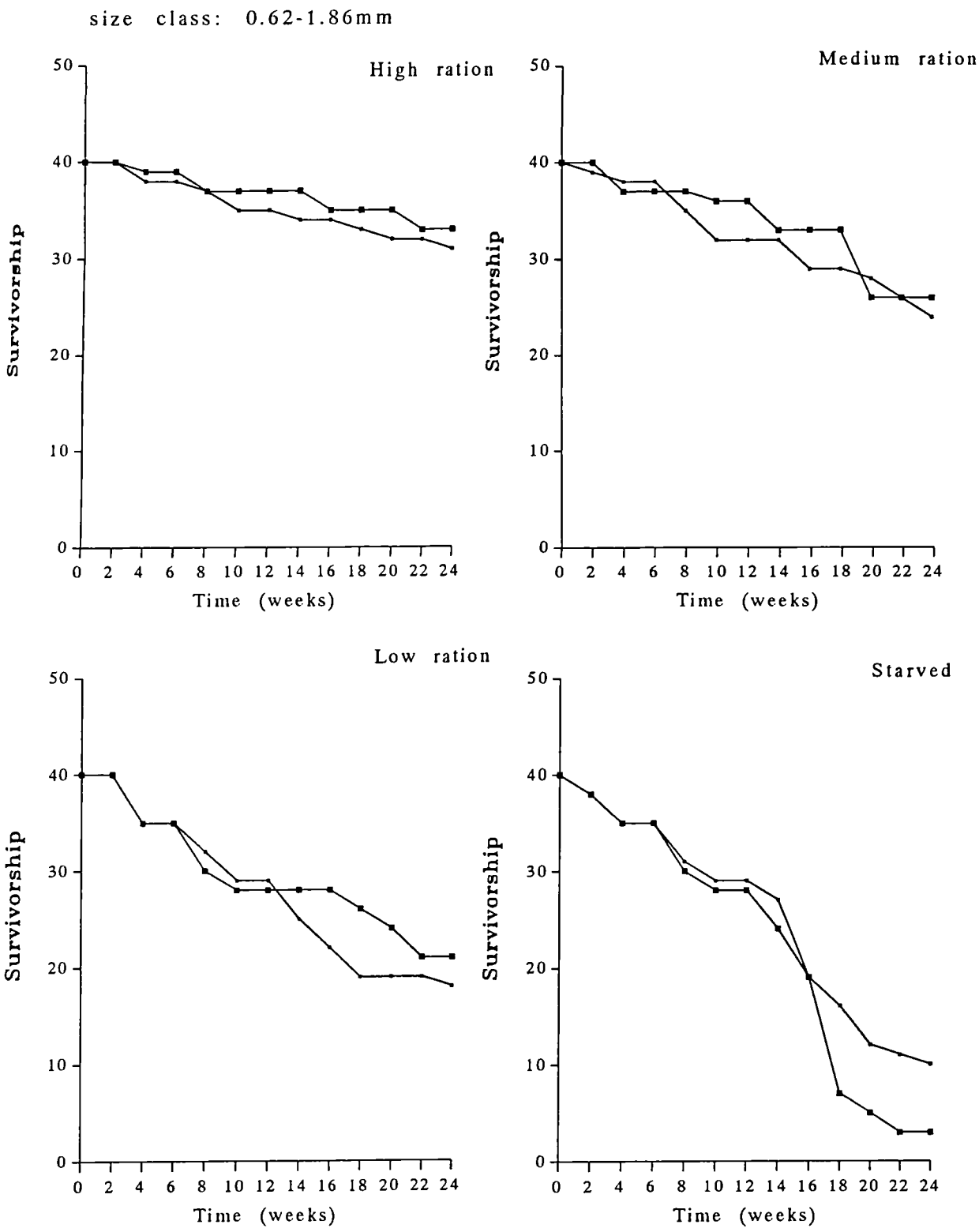


Figure 3.12: Survivorship curves of strain A and C large juveniles in the above regimes over a 24 week period.

ze class: 1.87-3.04mm

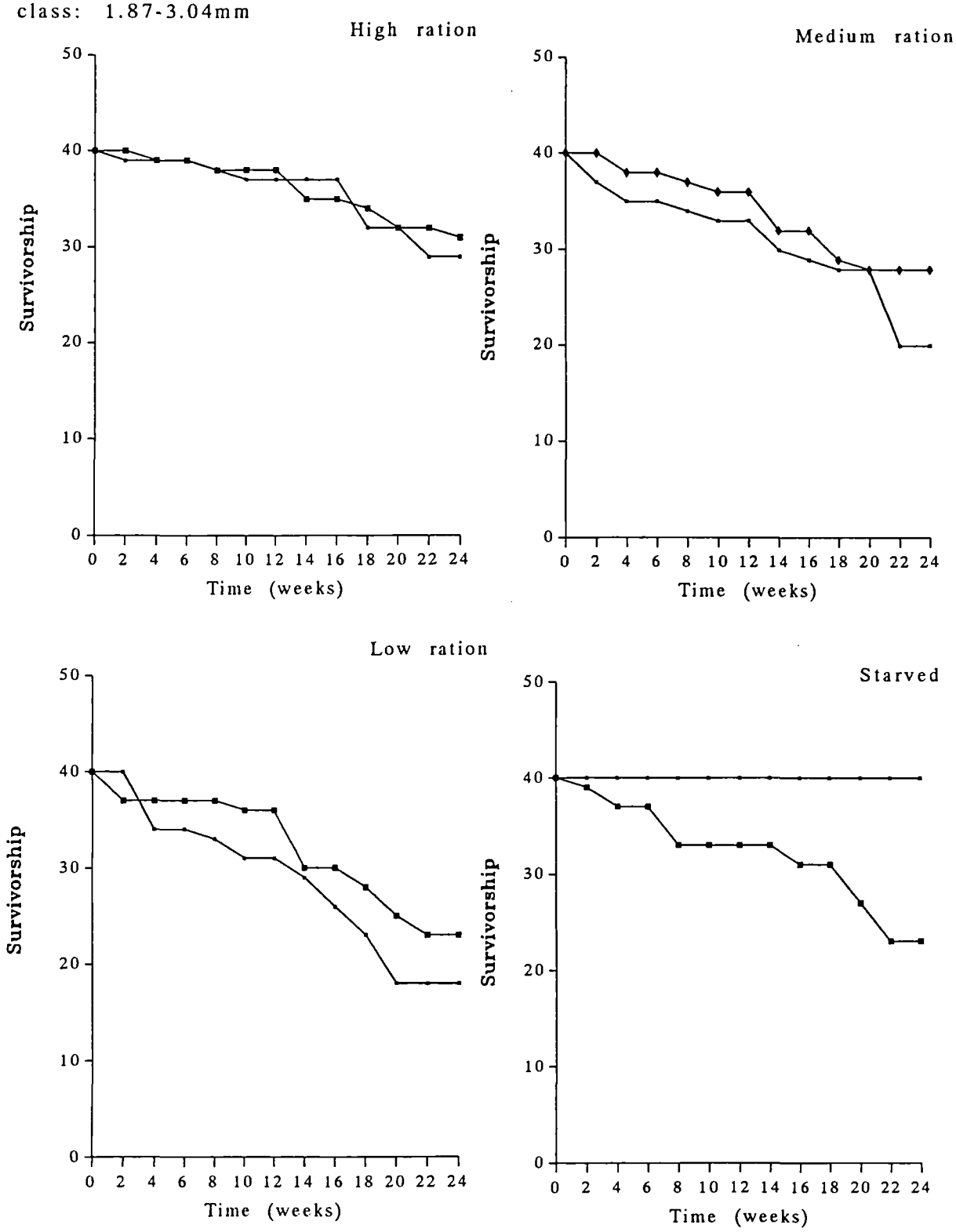


Figure 3.13: Survivorship curves of strain A and C adults in the above feeding regimes.

Table 3.11: Survivorship analysis of newly released juveniles size class using Lee-Desu Statistic (D) for A) Overall and B) Pairwise Comparison between the strains in four feeding regimes. (*P=0.01-0.05,**P=0.01-0.005,***P=0.001-0.005, NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	3.132	1	0.0768
All Four Treatments	12.099	3	0.0071

B. Pairwise Comparison

Comparison	H	G	F	E	D	C	B	A
A	10.11***	4.08*	4.257*	NS	6.489*	6.985**	NS	---
B	12.754	NS	5.069	NS	7.718**	6.649*	---	
C	NS	NS	NS	NS	NS	---		
D	NS	NS	NS	NS	---			
E	NS	NS	NS	---				
F	NS	NS	---					
G	NS	---						
H	---							

Where:
A = Strain A fed; B = strain A, medium ration; C = Strain A,low ration; D = Strain A, starved; E = Strain C, fed; F = Strain C, medium ration; G=Strain C, low ration; H = Strain C, starved.

Table 3.12: Survivoship analysis using the Lee-Desu Statistic (D) for A) Overall and B) Pairwise Comparison between strains A and C in four feeding regimes in the large juvenile size class. (*P=0.01-0.05,**P=0.005-0.01,***P = < 0.005,NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	0.366	1	0.5454
All Four Treatments	79.811	3	0.0000

B. Pairwise Comparison

Comparison	H	G	F	E	D	C	B	A
A	32.97***	6.71**	NS	NS	38.19***	10.18*	NS	---
B	17.05	NS	NS	4.58*	20.18**	NS	---	
C	NS	NS	4.76*	12.3***	4.17*	---		
D	NS	12.01**	28.93***	42.19***	---			
E	36.63***	8.37**	NS	---				
F	24.44***	NS	---					
G	9.56***	---						
H	---							

Where:
A = Strain A fed; B = strain A, medium ration; C = Strain A,low ration; D = Strain A, starved; E = Strain C, fed; F = Strain C, medium ration; G=Strain C, low ration; H = Strain C, starved

Table 3.13: Survivorship analysis using the Lee-Desu Statistic (D) for an A) Overall and B) Pairwise Comparison of strain A and C adults in four feeding regimes. (*P=0.01-0.05, **P=0.005-0.01, ***P < 0.005, NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	0.230	1	0.6315
All Four Treatments	13.167	3	0.0043

B. Pairwise Comparison

Comparison	H	G	F	E	D	C	B	A
A	18.16*	NS	NS	NS	NS	7.69**	NS	---
B	NS	NS	NS	7.96**	4.53*	NS	---	
C	NS	NS	4.93*	11.51**	7.34**	---		
D	9.011***	NS	NS	NS	---			
E	14.56***	4.69*	NS	---				
F	6.17**	NS	---					
G	NS	---						
H	---							

Where:
A = Strain A fed; B = strain A, medium ration; C = Strain A,low ration;
D = Strain A, starved; E = Strain C, fed; F = Strain C, medium ration; G=Strain C, low ration; H = Strain C, starved

throughout the 24 weeks. Strain A releases no young when starved (see sections 3.413 and 3.423). Hence no trade-off occurs between survivorship and fecundity as is observed in strain C snails. Pairwise comparison tests of starved strain C with starved strain A snails showed a significant difference in survivorship, with strain A having the greater survivorship. As explained above, the greater survivorship is due to the non-release of young by the starved snails. Strain A snails on low ration released no young, yet their survivorship was less than those snails that were starved. This might have been due to the allocation of energy to the production of embryos which could not have been released, however, until feeding conditions improved.

3.423 Fecundity

The results from the starvation experiment suggested that there must be a threshold level of food supply before strain A releases young. Thus, strain A showed no release of young when starved, while strain C showed some reproductive output, (Figure 3.14). As in the starvation experiment, only the adult size class was reproductively active.

Strain C released young in all treatments while strain A released young in high and medium ration (Figure 3.14). Strain A therefore has a nutritional cut-off point, below which it will preferentially allocate resources to the soma. This is reflected in strain A's greater survivorship when starved compared with strain C (Figure 3.13). Although in both strains the number of young released decreased with decreasing food availability (Figure 3.14), strain C snails on medium ration and low ration released young two weeks ahead of clonemates on high ration.

The ANOVA performed on the two strains for high and medium ration showed that the total number of young released did not differ significantly among the strains (Table 3.14), and the release of young was not affected by food ration. At high food ration, strain C released more young than strain A, whereas in the starvation experiment it was strain A that released more young. The difference may be explained in the initial sizes of the two strains, which were different from those in the starvation experiment,

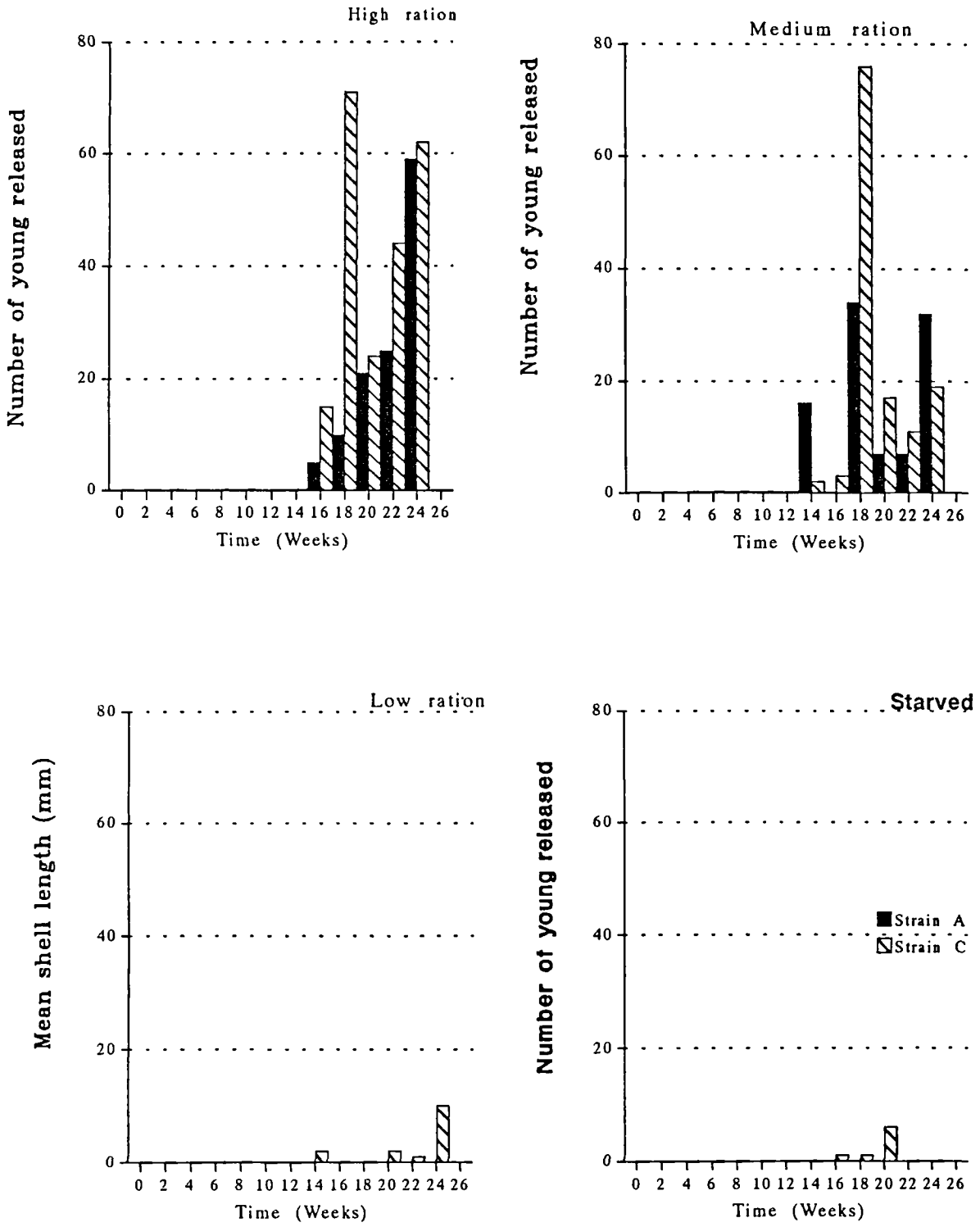


Figure 3.14: Total fecundity of strain A and C in the above feeding regimes. Only adult snails released young.

Table 3.14: ANOVA of the total fecundity between strain A and C in high and medium ration, as both strains released young in these two feeding treatments.

SOURCE	SEQ SS	ADJ SS	ADJ MS	D.F.	F	P
STRAIN	1430	1440	1440	1	0.71	0.42
TREAT	63	59	59	1	0.03	0.87
STRAIN*TREAT	8	8	8	1	0.00	0.95
ERROR	22201	22201	2018	11		
TOTAL	23702			14		

Table 3.15: One way ANOVA of strain C on the effect of four feeding environments (high, medium, low ration and starved) to its total fecundity. Strain C released young in all four treatments unlike strain A (refer to text).

SOURCE	SS	MS	D.F.	F	P
TREAT	7920	3960	2	5.67	0.007
ERROR	27240	698	39		
TOTAL	35160		41		

causing the snails to take longer to reach reproductive maturity. Because strain C released young in all four treatments a One-way ANOVA was performed (Table 3.15) which showed that as the food availability decreased the number of young released by the snails decreased by a significant amount.

3.5 DISCUSSION

It is generally accepted (eg Lynch 1980, Taylor; 1985) that well-nourished individuals attain a larger size than those raised on restricted ration, and this was found to be the case in the present study. However, genotypic differences in response to nutrition were evident. In the large juvenile size class, strain A fared better in well fed environments and strain C in poorer feeding environments (Figure 3.10).

Significant response to the environment in both the starvation and food ration experiments indicated phenotypic plasticity. Moreover, the overall interactions of **STRAIN x TREATMENT** and **STRAIN x TREATMENT x TIME** in the large juvenile and adult size classes were significant. Thus showing that the strains (genotypes) differed in their plastic responses (Schlicting, 1986). These interactions are important in showing that the relative fitness of the strains (with regard to growth) vary according to the environment. Only the newly released juvenile size class showed no response of phenotype to the environment. This was to be expected as growth of juveniles, even of different species, are generally similar (Spight and Emlen, 1976). On the other hand, the length of the juvenile period tends to differ, as also does the allocation of energy resources to different functions (Spight et al; 1974). Thus in the present case as the strains matured, they began to react differently to environmental conditions. Strain C large juveniles allocated most of its resources to growth and the adults to reproduction, whereas strain A, allocated most of its resources to somatic maintenance.

During this investigation it was observed that as the level of food decreased, the

young were released earlier. The advantage of delaying the release of young when well fed is shown in *Thais lamellosa* (Spight and Emlen, 1976). When food is abundant, they adjust to the supply by increasing their growth and thereby increasing their clutch size. Phenotypic plasticity of strains A and C extended to fecundity and survivorship. Importantly, in life histories there often exists a trade-off between fecundity and survivorship where an increase in reproduction is compensated by a decrease in longevity. The two strains demonstrated differences in reproductive tactics when placed under food stress and in the case of strain C at a cost to survivorship. Kaitala (1991) found similar results between a Finnish and Hungarian population of waterstrider. Both populations adopted different reproductive behaviour when present in high and low food levels and both were plastic to the environmental changes. As shown in the present study those individuals that released young in low food levels did so at the cost of a shorter life-span.

When food was rationed, the median life span of strain C snails was reduced (see appendix 2, section 2.26) while they continued to release young. Strain A had a longer median life span (see appendix 2, section 2.26), but ceased releasing young when food ration was too low. Brown (1982) working on brine shrimp, *Artemia*, found a positive correlation between female reproductive rate and longevity under good feeding conditions. But at low food levels the reduction in fecundity, achieved by keeping females unmated for varying lengths of time, was associated with an increase in mean life span. Similarly, Calow (1977), found virgin and mated water boatmen, *Corixa*, to have the same mean life span as when fed, although virgins lived longer when both were starved.

Strain A is solely found in inland waters, but is known to coexist with strain C in brackish waters. The observed difference in the trade-off between reproduction and longevity may indicate different reproductive tactics that may allow for coexistence of the strains. Thus the two strains were shown to change their reproductive allocation

differently according to the level of food supply. Although both showed poorer growth under low food level, strain A ceased releasing young whereas strain C continued to do so, albeit at a reduced rate. The high reproductive output of strain C was achieved at the cost of lower survivorship, as shown by the pairwise comparison test between fed and starved strain C snails (D-statistic = 16.241, D.F.= 1, P= 0.0001) and when the feeding regimes were varied (Table 3.13).

Strain A, under normal conditions, puts its resources into growth, with a consequently delayed release of young. But because of its larger final size, the cumulative number of young released by strain A is greater (Figure 3.7). Strain C strategy is to mature early, and when under food stress at a cost of a lower life-time reproductive output.

The earlier reproductive maturity of strain C may give it a temporary, preemptive advantage over strain A in the exploitation of ephemeral or newly colonised habitats. Juvenile mortality of strain C, when well fed, is not as great as that of juvenile strain A. Thus, the larger number of young released by strain A may compensate the high mortality that its newborn are likely to face (Figure 3.14). But with limited food supply, it is strain A juveniles that survive better than strain C juveniles (Figure 3.11). This is possibly due to the cost of growth in strain C snails.

In summary, when food is limited or absent, both strains show reduced growth. In the adults size class, not only did the growth in strain A cease, but also the release of young. Strain C, however, showed both the release of young and some growth. Thus under food stress, strain A snails give priority to somatic maintenance while strain C gives priority to reproduction.

CHAPTER 4:

RESPONSE TO SALINITY CHANGES

SUMMARY

The effect of increased salinity on the growth, survivorship and fecundity of strain A and C was investigated. Both strains showed increased growth and size in 5% and 10%SW. Higher salinities caused a reduction in growth. Reproduction in strain A ceased in 20%SW and above. Strain C released young in all salinities but at a cost to survivorship. The greatest cost was experienced at 10%SW, where strain C released the most young.

Both strains were plastic to increased salinity in their growth and fecundity. Significant **STRAIN x TREATMENT** interaction demonstrated the strains to differ in their plasticity and hence fitness in response to salinity increase.

4.1 INTRODUCTION

As mentioned in the preceding chapters strains A and C are found in inland freshwaters and estuaries respectively, although strain A can also be found in estuaries along with strain C (Warwick, 1952). Workers (e.g. Boycott, 1936, Johnson, 1981) have shown *Potamopyrgus jenkinsi* to tolerate a wide range of salinities. Johnson (1981) showed the tolerance of strain B to be greater than strain A in higher salinities. Todd (1964) and Duncan (1967) have shown *Potamopyrgus jenkinsi* to be able to cope with changes in salinities by producing a euryhaline urine, accompanied by an elevated respiration rate. However, the response of other phenotypic traits e.g. growth has not been hitherto considered in detail for either strain.

How the strains change their life-history traits in response to changes in salinity is important in understanding why strain A and C normally occupy separate habitats. The physiology of one strain may limit its expansion to more saline waters. Hence, the more plastic a genotype is with regard to its phenotype, the more likely it is to out-compete a genotype adapted to only one of the environments (Stearns, 1982; Thompson, 1991). Reaction norms (Schmalhausen, 1949), which plot phenotypic expression of a genotype over a range of environmental conditions will be considered. As discussed in chapter 3, *Potamopyrgus jenkinsi* is well suited to this type of analysis because each genotype (clone) can be exposed to all treatments at once.

The following investigation uses snails from stocks whose mothers were from separate habitats. Strain A snails were collected from the Llansadwrn stream (SH551767) while strain C snails were collected from the pond at Llanfairfechan (SH 678754). These habitats are fully described in chapter 5. Manipulating the environment by controlled changes in salinity should reveal the phenotypic plasticity of the two strains with regard to this characteristic environmental variable.

4.2 MATERIALS AND METHODS

Snails of the two strains A and C were graded into the same size classes as in chapter 3: newly released juveniles (0-0.61mm), large juveniles (0.62-1.86mm) and adults (1.87-3.04mm). Fifty snails from each size class were placed in solutions of 5%, 10%, 20% and 40% seawater (SW). The differing salinities were achieved by appropriately diluting 100% seawater (32‰) with copper-free freshwater. As a control, snails from each size class were placed in freshwater.

4.21 Growth

Each week, for a period of 21 weeks, the shell length was measured using a binocular microscope as described in chapter 1, with the graticule units calibrated to mm.

Statistical comparisons of the growth rates and the mean shell length of the two strains at the end of 21 weeks were made using univariate, nested repeated measures MANOVA (SPSS) as described in 3.21.

4.22 Survivorship

Each week, dead snails were counted and removed from the experimental containers. For each of the three size classes, differences between the two strains were compared using Survivorship Analysis (SPSS) and the Lee-Desu statistic. Details of this analytical methods are described in chapter 2.

4.23 Fecundity and Size at Maturity

The number of young released each week was recorded. Also recorded was the age and mean shell length of the parental snails when they first released any young. ANOVA (MINITAB) was used to analyse the data.

4.3 RESULTS

4.31 Growth

The growth curves of the three size classes of strain A and C are shown in Figure 4.1-4.3. MANOVA revealed a significant effect (Table 4.1-4.3) of salinity on the mean final shell length in the three size classes. In all cases except for strain C in the large juvenile size class (Figure 4.1), the snails present in 5%, 10% and 20%SW grew faster and became larger than those in the control treatment. Only in 40%SW was the growth and the final mean shell length sometimes found to be less than in the control.

Although salinity had a significant effect on the final shell length of the snails, no significant difference was shown in this variable between the strains in the juvenile size classes (Table 4.2). Only the adults showed a significant difference (MANOVA, $F_{1,4}$= 6.50, P= 0.015). However, there was a significant difference in the strains' growth in the adult and newly released juvenile snails.

The strains in the two larger size classes differed in their response to treatment as shown by the significant STRAIN x TREATMENT interaction. The crossing of the reaction norms in the large juvenile size class (Figure 4.4A) shows the strains to be greatly affected by the environment. Strain C showed a positive response to increasing salinity, while strain A showed a positive response in 5%SW, but to further increases it showed a negative response. In the adult size class, strain A showed very little response to salinity increase (Figure 4.4B), its size only decreasing slightly at 40%SW. On the other hand, strain C demonstrated a positive response at 5%SW, then showed a strong decrease in size to 20%SW. The reaction norms did not cross so, indicating a genotypic main effect.

size class: 0-0.61mm

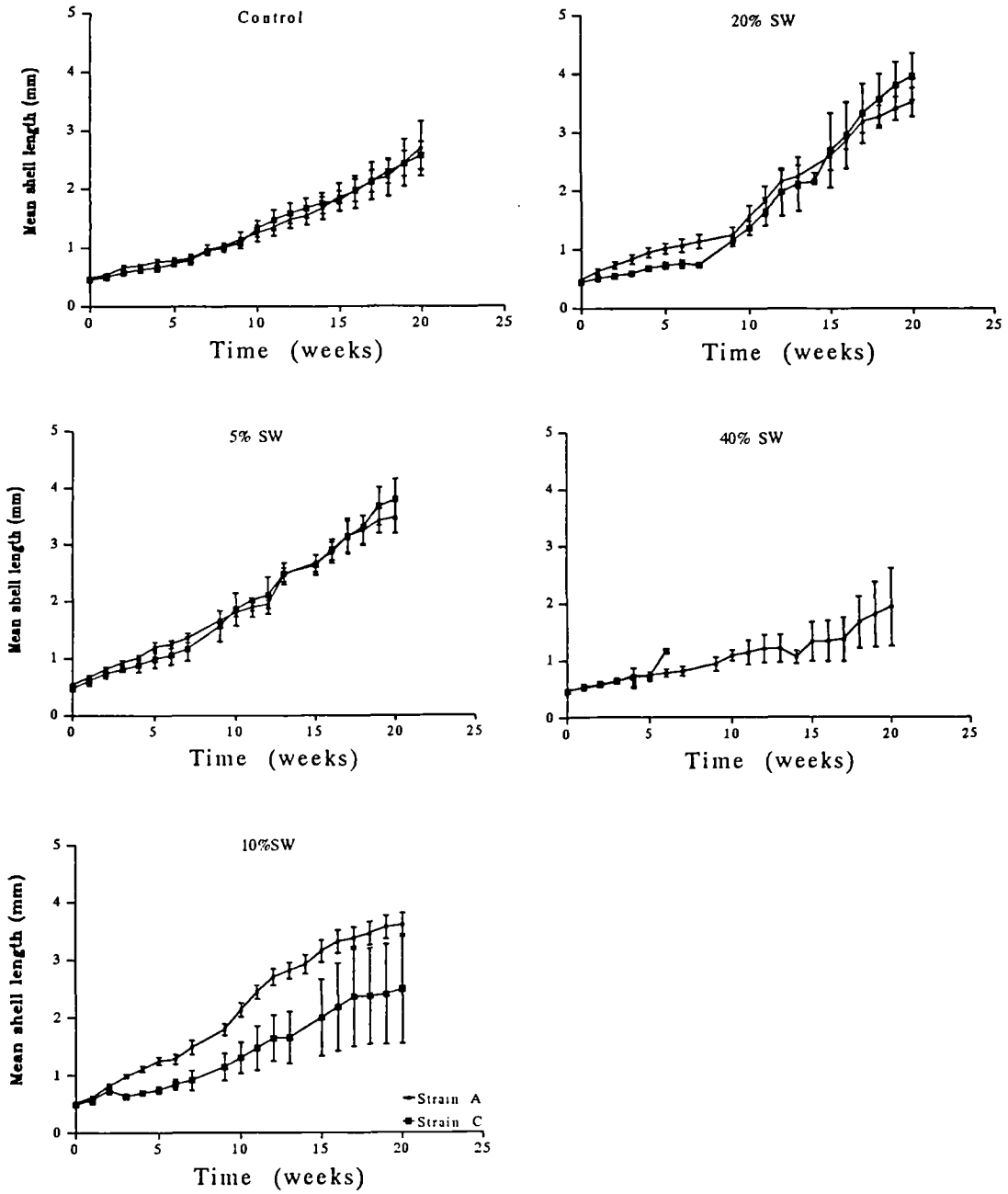


Figure 4.1: Growth of strain A and C newly released juveniles in varying salinities for the period of 20 weeks. Points are means, vertical lines error bars.

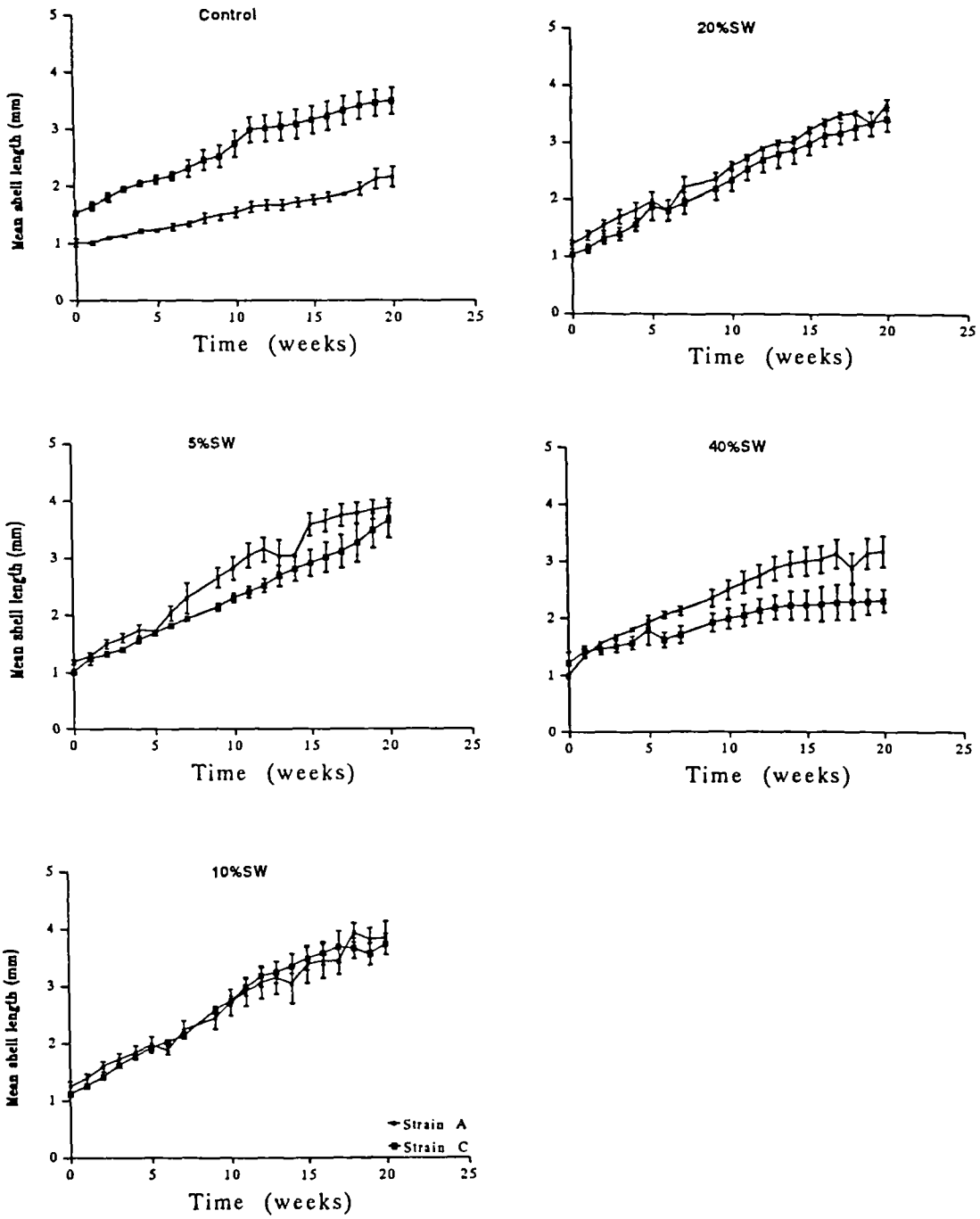


Figure 4.2: Growth of strain A and C large juvenile snails in varying salinities for the period of 20 weeks.

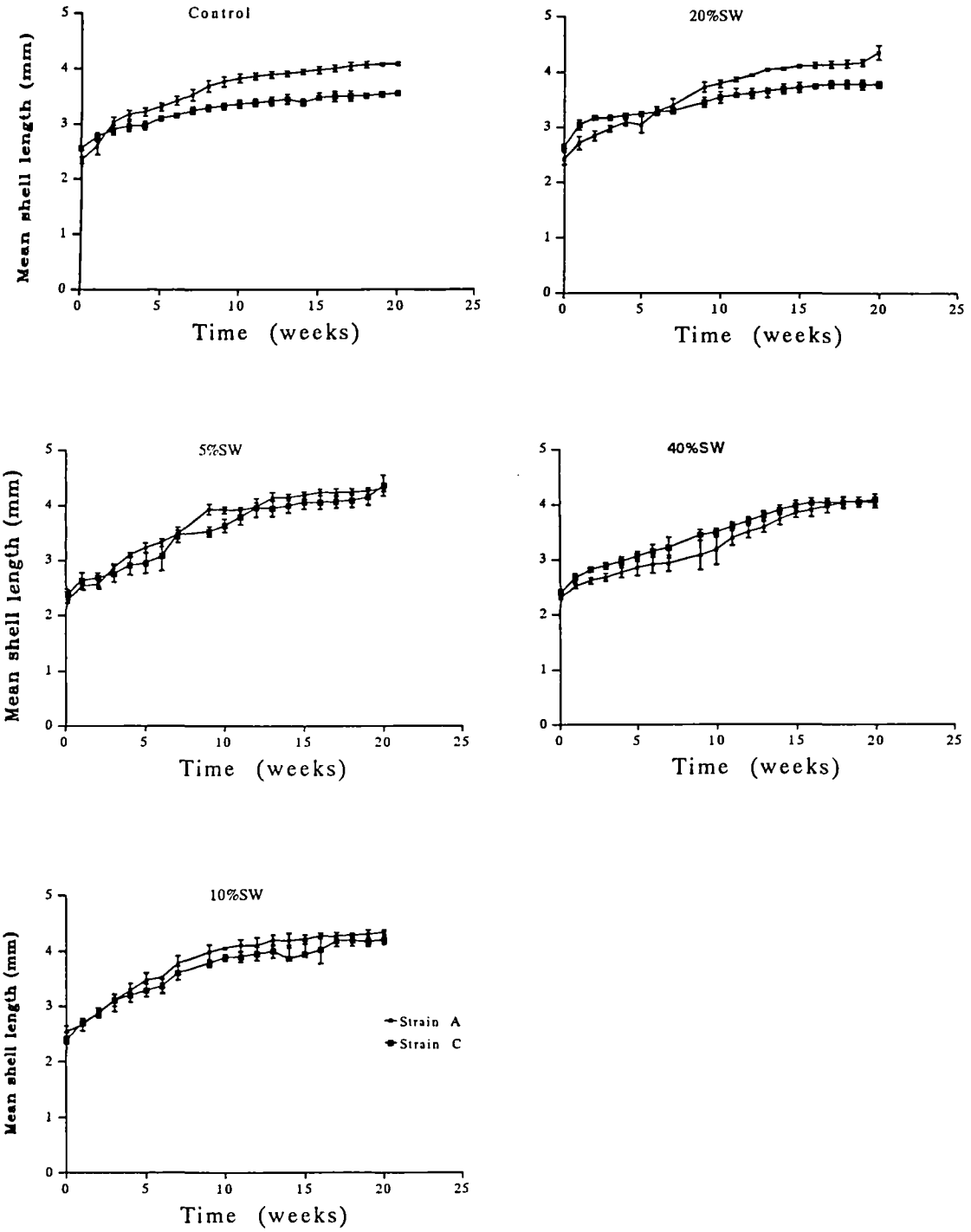


Figure 4.3: Growth of strain A and C adults in varying salinities over a period of 20 weeks. Points are means, vertical lines standard error bars.

Table 4.1: Nested MANOVA (SPSS) on the effect of varying salinity on growth and overall mean shell length (mm) in newly released juvenile strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	1.50	1	1.50	1.04	0.314
TREAT	34.93	4	8.73	6.03	0.001
STRAIN BY TREAT	12.51	4	12.51	2.16	0.091
ERROR 1	57.96	40	1.45		
TIME	268.89	5	53.78	934.53	0.000
TIME BY STRAIN	1.14	5	0.23	3.98	0.001
TIME BY TREAT	29.66	20	1.48	25.77	0.000
STRAIN BY TREAT BY TIME	7.69	16	0.48	8.35	0.000
ERROR	34.70	603	0.06		

Table 4.2: Nested MANOVA (SPSS) on the effect of varying salinity on growth and overall mean shell length (mm) in large juvenile strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	0.01	1	0.01	0.01	0.941
TREAT	40.44	4	10.11	7.84	0.000
STRAIN BY TREAT	51.59	4	12.90	10.01	0.000
ERROR 1	51.56	40	1.29		
TIME	448.40	5	89.68	1632.80	0.000
TIME BY STRAIN	0.21	5	0.04	0.75	0.588
TIME BY TREAT	27.55	20	1.38	25.08	0.000
STRAIN BY TREAT BY TIME	9.85	20	0.49	8.97	0.000
ERROR	40.53	738	0.05		

Table 4.3: Nested MANOVA (SPSS) on the effect of varying salinity on growth and overall mean shell length (mm) in adult strain A and C snails.

Source of Variation	SS	D.F	MS	F	P
STRAIN	2.65	1	2.65	6.50	0.015
TREAT	14.35	4	3.59	8.79	0.000
STRAIN BY TREAT	8.16	4	2.04	5.00	0.002
ERROR 1	16.32	40	0.41		
TIME	233.44	5	46.69	1165.65	0.000
TIME BY STRAIN	3.73	5	0.75	18.61	0.000
TIME BY TREAT	10.61	20	0.53	13.25	0.000
STRAIN BY TREAT BY TIME	4.02	20	0.20	5.02	0.000
ERROR	29.68	741	0.04		

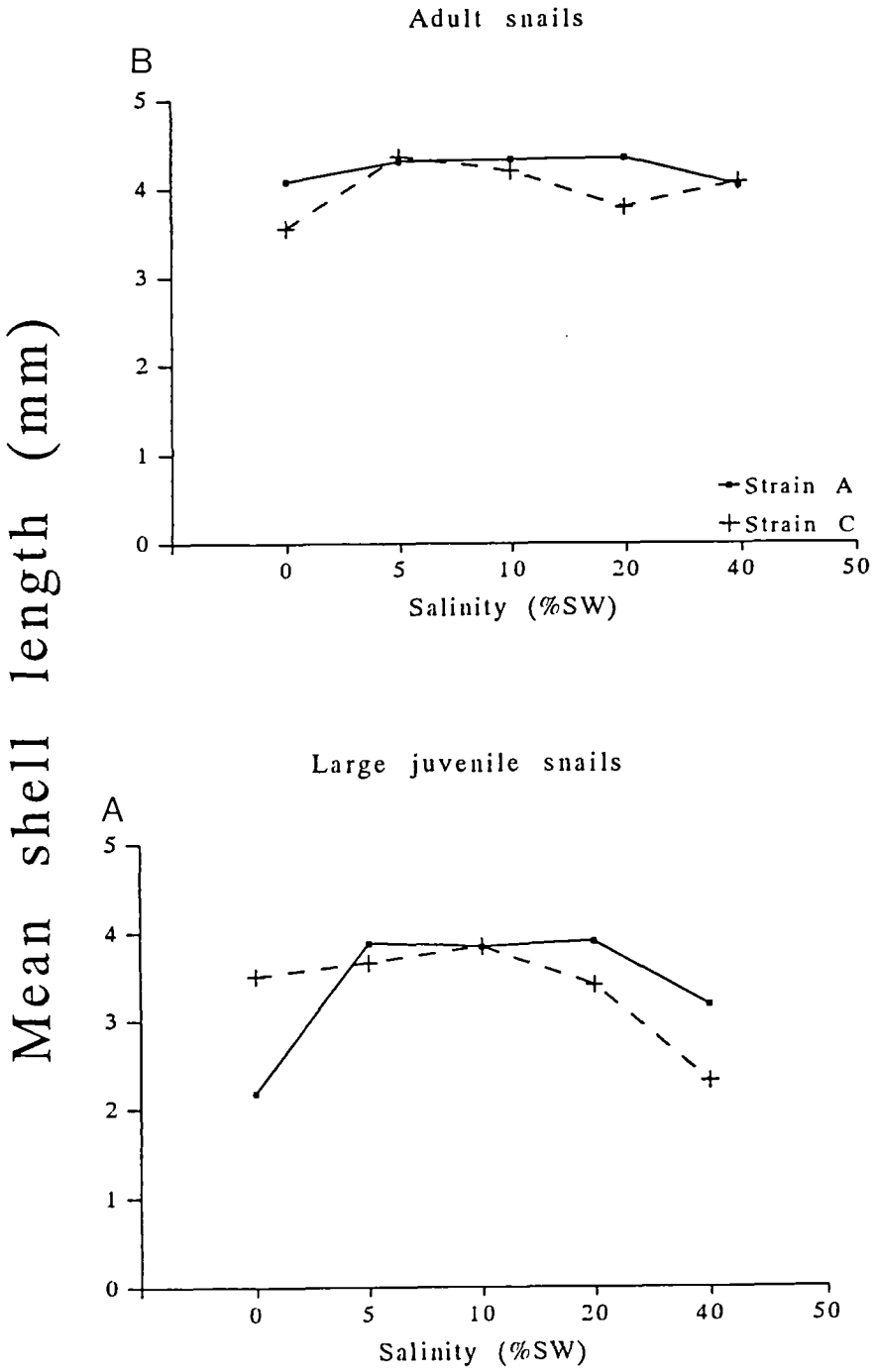


Figure 4.4: Reaction norms of strain A and C large juvenile and adult snails in varying salinity.

4.32 Survivorship

An increase in salinity caused a significant reduction in the survivorship of the newly released juvenile snails (Figure 4.5, Table 4.4A). However, the overall survivorship of the two strains was shown to be similar (Table 4.4A).

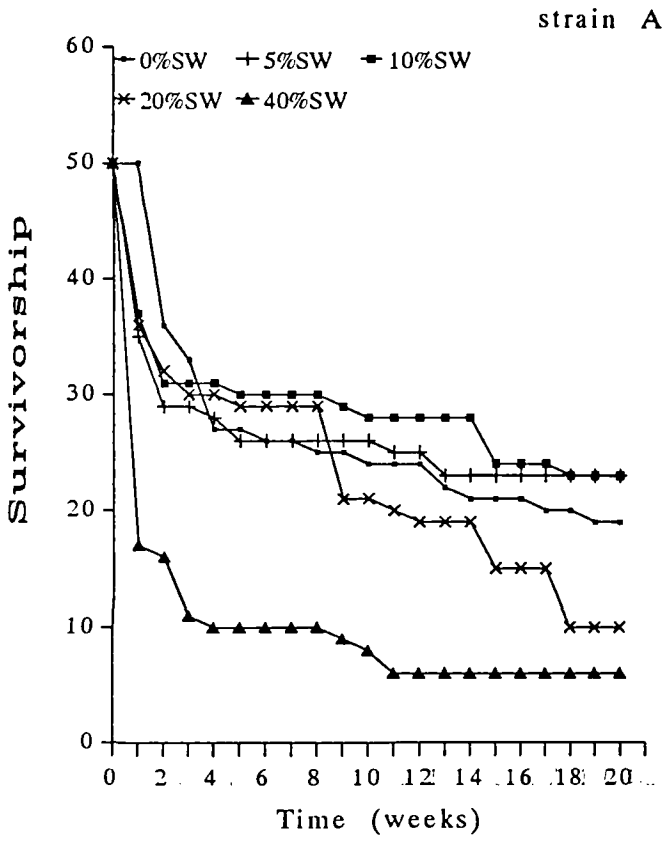
Pairwise comparison tests between the two strains showed strain A to have the greater survivorship (see also appendix 2, section 2.31 with life tables). Only the survivorship of strain C snails in the control was greater when compared to snails in the test salinities.

Figure 4.6 shows the survivorship of the large juvenile size class. The survivorship of strain A was significantly greater than strain C (D-statistic= 5.16, D.F.=1, P= 0.023). A significant difference was also found when the overall effect of salinity on the snails survivorship was examined (D-statistic= 20.87, D.F.= 4, P= 0.003). Pairwise comparison tests showed the survivorship of strain A to be similar in all salinities (Table 4.5B). Also revealed were similarities between the strains when compared in each treatment. However, the survivorship of strain C snails in 5%SW, was significantly less when compared to strain A in the various test salinities (see life tables in appendix 2, section 2.32 for median life span).

As in the newly released juvenile size class, no significant difference in survivorship was found between the two strains in the adult size class (Figure 4.7, Table 4.6A). Yet the snails overall survivorship was significantly affected by salinity concentration (Table 4.6A).

Pairwise comparison tests (Table 4.6B) showed the survivorship of strain A to be similar in all five environments. A significant decrease in the survivorship of strain C snails was demonstrated in the order of 0%SW > 5%SW > 40%SW > 10%SW (see appendix 2, section 2.33 for median life span). The decrease is in this order because strain C shows the greatest output of young in 10%SW (see section 4.34 and Figure 4.8) and the least in 40%SW. So the cost to survivorship is greater at 10%SW than at 40%SW. Nonsignificant differences were found in the comparison of the strains in each of the test

size class:0-0.61mm



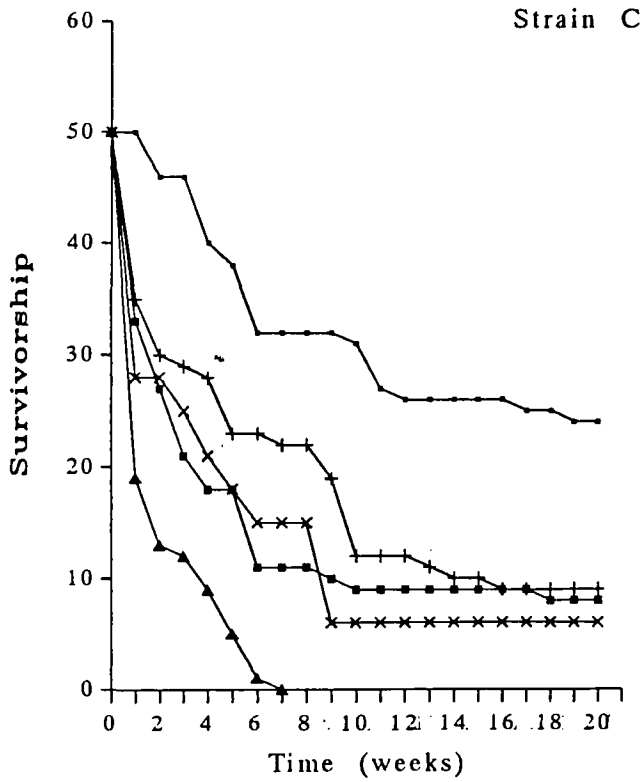


Figure 4.5: Survivorship curves of strain A and C newly released juveniles 5 salinities over 20 weeks.

size class: 0.62-1.86mm

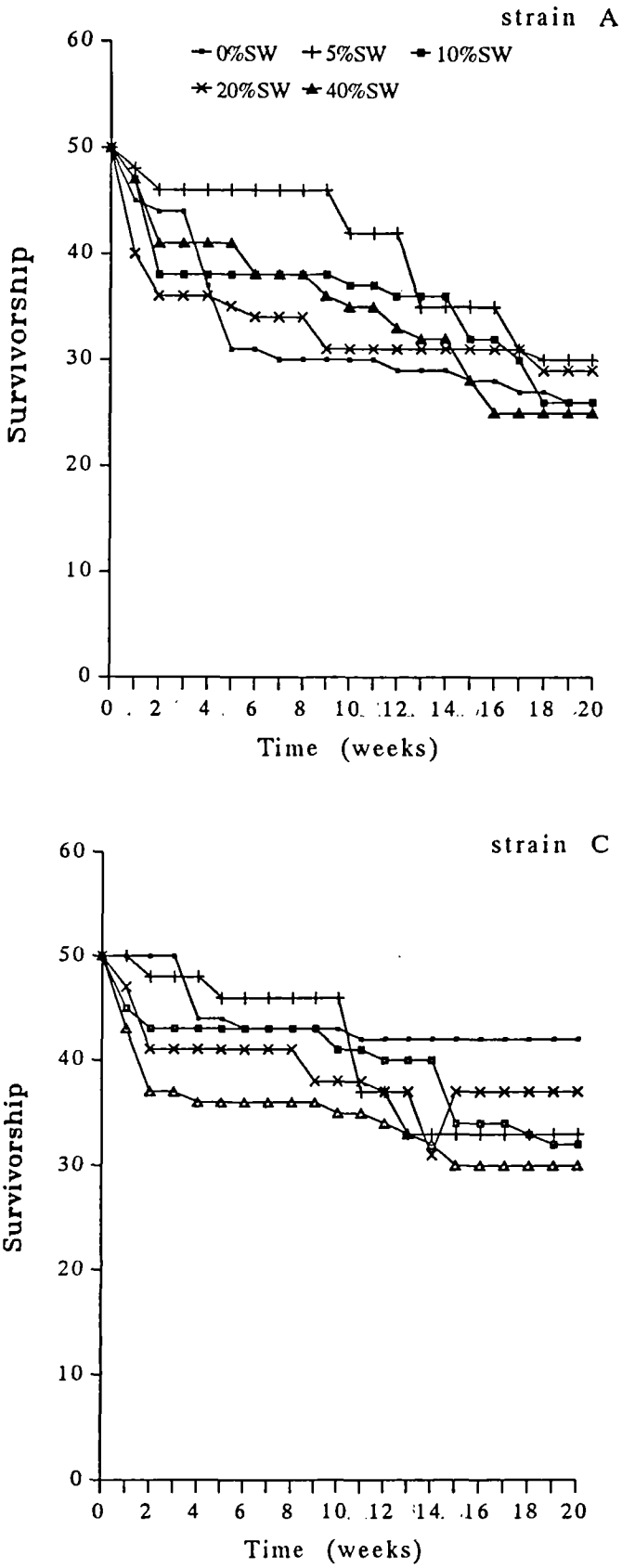


Figure 4.6: Survivorship curves of strain A and C large juvenile snails in five salinities. Salinities are expressed as % seawater

size class: 1.87-3.04mm

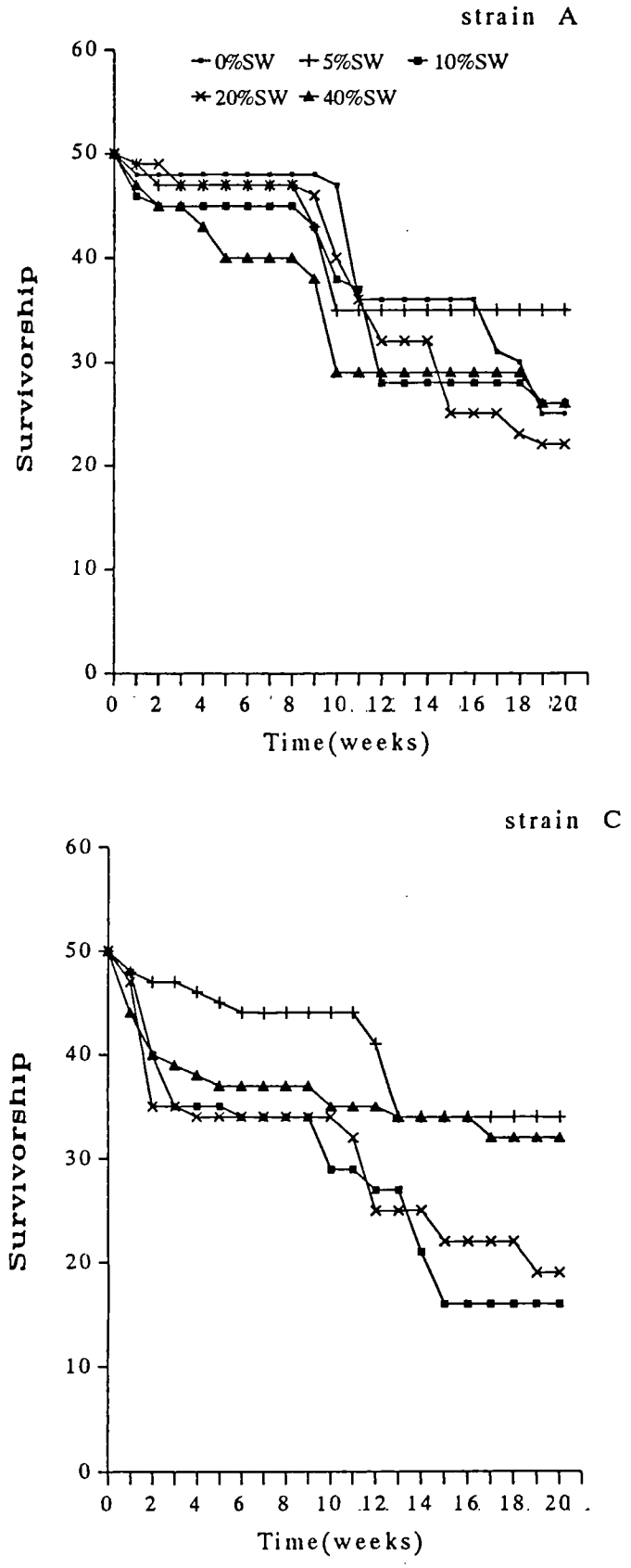


Figure 4.7: Effect of varying salinity on the survivorship of adult strain A and C snails.

Table 4.4: Survivorship analysis using the Lee-Desu D-Statistic for an A) Overall and B) Pairwise Comparison of strain A and C newly released juveniles in varying salinity regimes. (aP=0.01-0.05, bP=0.005-0.01, cP < 0.005, NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	1.21	1	0.27
All Five Salinities	55.73	4	<0.005

B. Pairwise Comparison

Comparison	J	I	H	G	F	E	D	C	B	A
A	6.74^b	NS	NS	NS	25.37^C	6.88^b	NS	NS	NS	___
B	15.62^b	6.2^b	NS	NS	11.57^c	14.87^c	NS	NS	___	
C	22.16^c	9.88^c	6.40^a	9.28^c	18.04^c	NS	NS	---		
D	19.95^c	5.80^a	NS	NS	20.74^c	12.52^c	---			
E	NS	NS	5.90^a	9.69^c	47.82^c	---				
F	57.76^c	38.08^c	35.26^c	26.16^c	---					
G	13.11^c	NS	NS	---						
H	4.00^a	NS	---							
I	NS									
J	---									

Where:
A = Strain A, 0%SW (control); B = strain A, 5%SW; C = Strain A,10%SW; D = Strain A, 20%SW; E = Strain A, 40%SW; F = Strain C, 0%SW (control); G=Strain C, 5%SW; H = Strain C, 10%SW; I= Strain C, 20%SW; J=Strain C, 40%SW.

Table 4.5: Survivorship analysis using the Lee-Desu D-Statistic for an A) Overall and B) Pairwise Comparison of strain A and C large juveniles in varying salinity regimes. (aP=0.01-0.05, bP=0.005-0.01, cP < 0.005, NS= Not significant)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	5.16	1	0.023
All Five Salinities	20.87	4	<0.005

B. Pairwise Comparison

Comparison	J	I	H	G	F	E	D	C	B	A
A	NS	NS	NS	18.66[c]	NS	NS	NS	NS	NS	___
B	NS	NS	NS	19.58[c]	NS	NS	NS	NS	___	
C	NS	6.14[c]	NS	25.51[c]	NS	NS	NS	---		
D	NS	6.65[b]	NS	27.25[c]	NS	NS	---			
E	NS	6.55[a]	NS	24.52[c]	NS	---				
F	NS	14.97[c]	9.34[c]	47.33[c]	---					
G	22.2[C]	11.1[c]	61.50[c]	---						
H	NS	NS	---							
I	4.70[a]									
J	---									

Where:
A = Strain A, 0%SW (control); B = strain A, 5%SW; C = Strain A,10%SW; D = Strain A, 20%SW; E = Strain A, 40%SW; F = Strain C, 0%SW (control); G=Strain C, 5%SW; H = Strain C, 10%SW; I= Strain C, 20%SW; J=Strain C, 40%SW.

Table 4.6: Survivorship analysis using the Lee-Desu D-Statistic for an A) Overall and B) Pairwise Comparison of strain A and C adults in varying salinity regimes. (aP=0.01-0.05, bP=0.005-0.01, cP < 0.005)

A. Overall Comparison	D	DF	P
Strain A vs Strain C	0.16	1	0.69
All Five Salinities	24.95	4	<0.005

B. Pairwise Comparison

Comparison	J	I	H	G	F	E	D	C	B	A
A	NS	NS	3.99[b]	NS	22.3[c]	NS	NS	NS	NS	___
B	NS	8.14[b]	10.89[b]	NS	8.09[b]	NS	NS	NS	___	
C	NS	NS	NS	NS	17.77[c]	NS	NS	---		
D	NS	NS	5.22[a]	3.93[a]	21.98[c]	NS	---			
E	NS	NS	NS	NS	17.68[c]	---				
F	11.83[c]	27.58[c]	31.17[c]	9.10[c]	---					
G	NS	10.018[c]	11.44[c]	---						
H	4.70[a]	NS	---							
I	NS									
J	---									

Where:
A = Strain A, 0%SW (control); B = strain A, 5%SW; C = Strain A,10%SW; D = Strain A, 20%SW; E = Strain A, 40%SW; F = Strain C, 0%SW (control); G=Strain C, 5%SW; H = Strain C, 10%SW; I= Strain C, 20%SW; J=Strain C, 40%SW.

salinities. It was expected that strain C would fare better in higher salinities. The results obtained could reflect the fact that strain C releases young in all treatments, hence causing its survivorship to drop and be similar to strain A snails in the corresponding salinities.

4.33 Fecundity and Size at Maturity

Reproductive activity was shown only in the largest size class of both strains. Strain C released young in all five treatments while strain A released young in all but 40%SW.

ANOVA performed on the total number of young released (Table 4.7A) showed the two strains not to differ significantly in fecundity and that salinity had a significant effect. In strain A the total fecundity decreased with increased salinity (Figure 4.8), while in strain C the total number of young released increased up to 10%SW and then decreased sharply at 20% and 40%SW. However, a significant **STRAIN x TREATMENT** interaction showed the effect of salinity to be dependent on the strain, although the variation between the strains is mainly caused by the the saline conditions. The oneway ANOVA (Table 4.7B) performed on strain C as it released young in five treatments, showed increasing salinity to effect the number of young released in the way described above.

The shell length at which the snails commenced releasing young differed significantly between the two strains (Table 4.8), with strain C snails releasing young at a smaller size (at 10%SW 3.89mm, S.E.=0.17mm) than strain A snails (at 10%SW 4.12mm, S.E.=0.01mm) (Figure 4.9). Salinity was also shown to effect the size at which the snails released young (ANOVA, $F=6.37_{3, 30}$, P= 0.002). The analysis did not include those snails in 40%SW, as strain A released no young at this salinity.

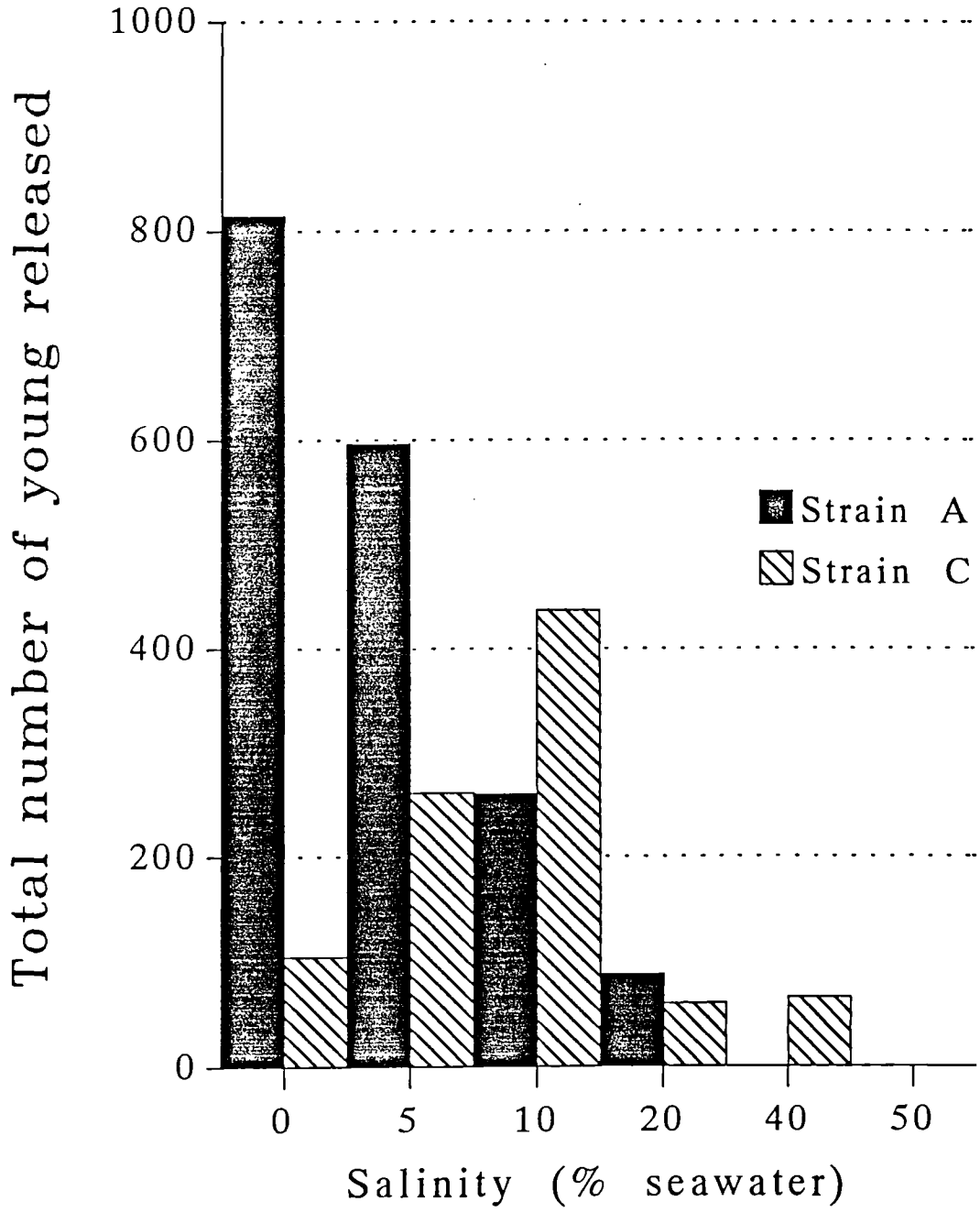


Figure 4.8: Effect of varying salinity on the number of young released by strain A and C snails.

Table 4.7: ANOVA of the total fecundity between strain A and C in 0%, 5%, 10% and 20%SW, as both strains released young in these four salinity treatments.

SOURCE	SEQ SS	ADJ SS	ADJ MS	D.F.	F	P
STRAIN	1003.8	855.4	855.4	1	1.68	0.197
TREAT	15646.6	1536.2	5120.9	3	10.06	0.000
STRAIN*TREAT	4470.2	4470.2	1490.1	3	2.93	0.037
ERROR	60587.4	60587.4	509.1	119		
TOTAL	81708.0			126		

Table 4.8: One way ANOVA of strain C on the effect of five salinity environments (0%, 5%, 10%, 20%, 40%SW) to its total fecundity. Strain C released young in all five treatments unlike strain A (refer to text).

SOURCE	SS	MS	D.F.	F	P
TREAT	6817.1	1704.3	4	4.93	0.002
ERROR	23522.9	345.9	68		
TOTAL	30340.0		72		

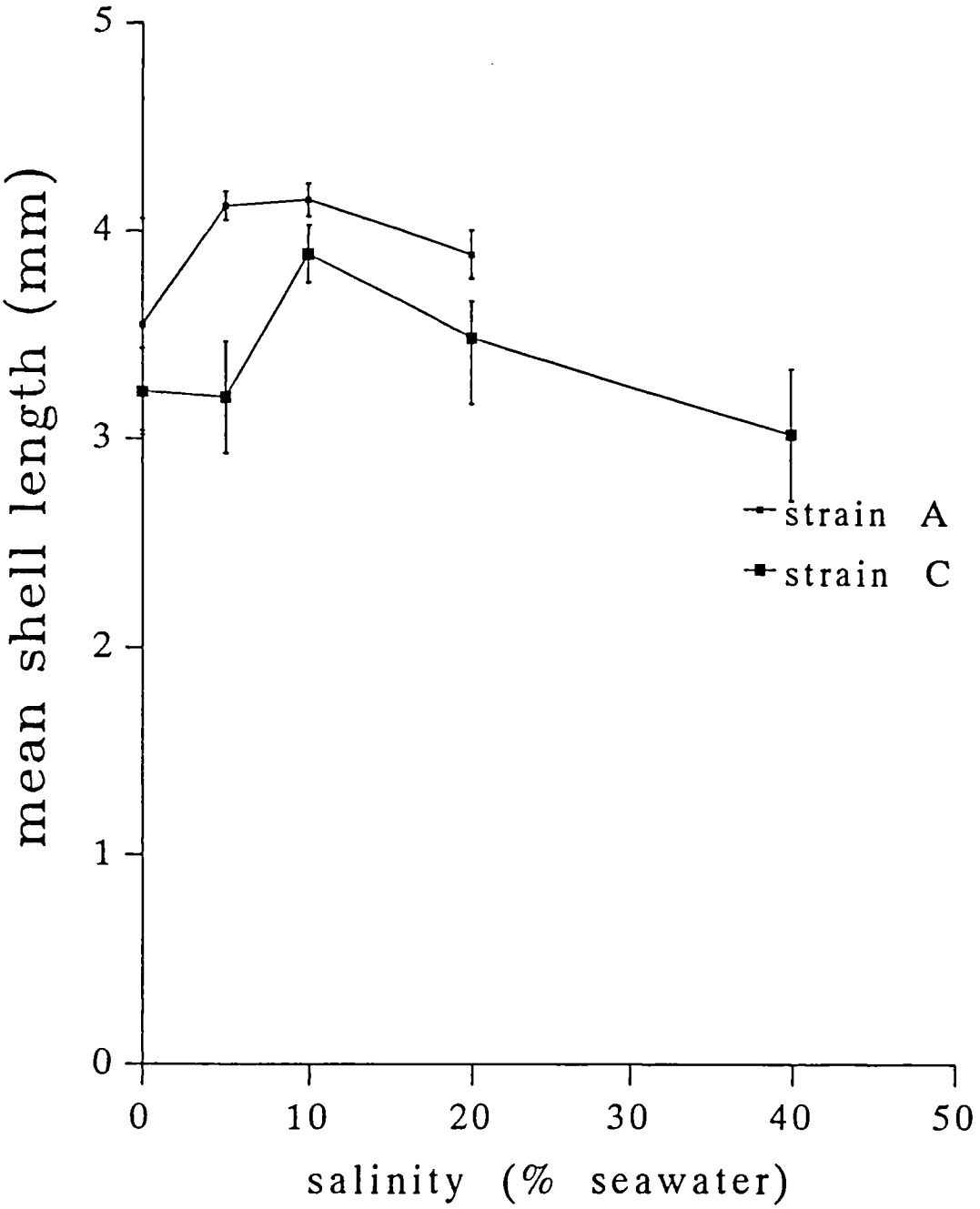


Figure 4.9: Effect of salinity on the size at which the two strains commence to release young. Size are mean shell lengths (in mm), and vertical lines standard error bars.

Table 4.8: ANOVA on the size (shell length, mm) at which the two strains first release young in 0%,5%,10% and 20%SW. Strain A released no young at 40%SW and so is not considered.

SOURCE	SEQ SS	ADJ SS	ADJ MS	D.F.	F	P
STRAIN	2.18	2.06	2.06	1	20.94	0.000
TREAT	1.88	1.88	0.626	3	6.37	0.002
STRAIN * TREAT	0.68	0.68	0.225	3	2.29	0.98
ERROR	2.95	2.95	0.098	30		
TOTAL	7.687			37		

4.4 DISCUSSION

Growth rate and the final mean shell length of both strains were greater in salinities of 5% to 10%SW than in freshwater. Duncan and Klekowski (1967) demonstrated that as salinity increased *Potamopyrgus jenkinsi* increased its respiratory rate, and believed this to be caused by the acceleration of growth. Thus, the possibility that *Potamopyrgus jenkinsi* originated from brackish waters (Bondesen and Kaiser, 1949; Ellis, 1969) could explain why the growth and the final mean size of the snails were generally greater in 5% and 10%SW than in freshwater.

However, in the case of strain C snails, the increased growth rate and final size at intermediate salinities was achieved at a cost of decreased survivorship. Those in the control had a longer life span and, in the case of the large juvenile size class, those present in 40%SW also showed an increased life span. There appeared to be a trade-off between increased growth and survivorship in the juvenile size classes, although this was not exhibited in the adult size class. Several authors (Adam, 1942; Bryan, 1963; Todd, 1964; Duncan, 1967) have shown adult *Potamopyrgus jenkinsi* from fresh and brackish waters to be fully active and feeding in salinities ranging from freshwater to 100% seawater.

The ability of *P. jenkinsi* to adapt to rapidly changing salinity was shown by Todd (1964). The snails adjust the osmotic concentration of their urine, which in all three strains, A,B and C (see chapter 1), remains hyperosmotic whether they are in freshwater or saline water. So if *P.jenkinsi* did originate from brackish waters, the progression to freshwater would only require small adjustments to existing osmoregulatory adaptations.

In the present study *P. jenkinsi* was shown to tolerate high salinities, the fecundity of the snails was adversely affected by increasing salinity, with strain A being unable to reproduce in salinities above 13.33‰(40%SW). Strain C continued to release young at higher salinities but had maximum fecundity at 10%SW. Duncan (1967) found that snails of unspecified strain ceased reproduction when salinity reached either 12‰or 18‰

which in this study was found to be the critical region for strain A.

Strain C snails showed the greatest reproductive effort when under stress and this was achieved at the expense of survivorship. As mentioned above, strain A ceased reproduction at 40%SW while strain C retained reproductive activity, even though at a reduced level. The fact that strain A ceased to release young at high salinities may explain why, when the two strains are found in the same environment, strain A is never found near the entry to the sea.

Both strains were found to be phenotypically plastic in their response to salinity changes. But the significant STRAIN x TREATMENT interaction in the two larger size classes demonstrates that the degree of response in the two strains differs. The STRAIN x TREATMENT interaction is also revealed by the reaction norms (Figure 4.4AB). If the reaction norms do not cross and one lies consistently above the other, as shown in the adult size class, then the corresponding genotype is superior in all environments (Stearns, 1989a). However, if they do cross (Figure 4.4A) then the phenotypic distributions provide no evidence for genetically based differences (Thompson, 1991), although a genotype may do better in one environment than the other.

It would appear that in the juvenile size class the effect of the environment is greater, while in the adults the differences in the genotype become apparent and have a stronger effect in the response of the snails.

In summary, increased salinity showed a decrease in growth in very high salinities (i.e. 20% and 40%SW) while in lower salinities (i.e. 5% and 10%SW) there was an increase in growth. Strain A is more sensitive to environmental cues of increased salinity and will cease its reproductive output. Strain C continues to release young and at a cost to survivorship. The effect of the environment is greatest on the large juvenile size class, but in the adults the underlying genotypic differences come into play.

CHAPTER 5:

POPULATION DYNAMICS OF STRAIN A AND C IN THEIR NATURAL HABITAT

SUMMARY

A year-long field study to investigate the size frequency distribution of strains A and C was undertaken. Adults present in the monthly samples were prised open to expose the brood pouch. The number of embryos present and their stage of development was noted and recorded.

The life-history characteristics of the two strains appeared to conform with predictions from the theory of 'r'- and 'K'-selection (Pianka, 1970), strain A approximating to a 'K'-selected organism and strain C to an 'r'-selected organism.

5.1 INTRODUCTION

Potamopyrgus jenkinsi was first recorded in England in 1889 from brackish waters of the Thames estuary and later spread to inland freshwaters throughout the British Isles. Its rapid dispersal has been well documented Bondeson and Kaiser (1949), Hunter and Warwick (1957), Fretter and Graham (1978). Its invasion of inland waters has been mainly due to passive dispersal by birds and fishes such as trout (Hubendick, 1950; Ribi, 1986), but also to some extent due to its own mobility (Heywood and Edwards, 1962).

The natural habitats of the two strains, A and C, of *Potamopyrgus jenkinsi* used in this study, show seasonal variation of environmental conditions. In the summer the habitat of strain A is choked by extensive vegetational overgrowth, while in the winter months the streams flow is rapid. Strain C snails experience greatest stress during the months of November to March, when the pond is extensively drained.

The selection pressures associated with contrasting environmental conditions in different habitats (e.g. water temperature and food availability) may influence the evolution of life-history traits. This may result in genetically based divergence (Stearns, 1976). Recent work has indicated that much of the intraspecific variation shown in life histories (e.g. Brown *et al.*, 1985; Etter, 1989; Crowl, 1990) is due to a plastic response to the environmental heterogeneity. In some cases this variation does have a genetic basis (e.g. Calow, 1981; Brown *et al.*, 1985). Only by separating phenotypic variation from genetic variation can a proper understanding of life-history pattern be gained (Stearns, 1976).

Gadgil and Bossert(1970) first suggested that the variations observed in life histories could be interpreted as adaptive strategies. Two main models have been developed to help explain such adaptive strategies. The first is a deterministic model (MacArthur and Wilson, 1967; Pianka, 1970), which proposes that populations inhabiting a stable environment have low intrinsic rates of increase, with few offspring, but that

each offspring is endowed with high energy reserves (K-strategy). On the other hand populations that inhabit variable environments have a higher intrinsic rate of increase, large numbers of offspring and all with small energy reserves (r-strategy).

The second is a stochastic model (Schaffer, 1974), which recognises that mortality and fecundity schedules vary. It predicts that when fluctuations in juvenile mortality are greater than in adults, the characteristics shown in 'K-'selection are found. But when adult mortality rates show the greater fluctuations, the characteristics shown in 'r'-selection are appropriate (Horn, 1978). Stearns (1976), following Schaffer, (1974), called this response to variable survivorship bet-hedging.

The previous chapters have shown the two strains A and C to vary in some of their life-history characteristics under controlled laboratory conditions and in their responses to experimental manipulations. However, in the naturally varying habitat, there are many factors that will ultimately affect growth and fecundity and hence population size-frequency structure.

To gain some insight [illegible], monthly samples were taken at both sites and the population size-frequency distributions recorded. Subsamples were used to investigate reproductive maturation and seasonal patterns of reproductive condition.

5.11 Habitats

Strain A was collected at Llansadwrn farm stream (ordnance survey reference SH 551767). The stream is narrow and richly vegetated on its banks. There is also a wide variety of organisms in the stream including gammarids, leeches and limpets. Between September and October, the average water depth is approximately 15cm. This rises to approximately 30cm between November and March. In these months the water is fast-flowing and is relatively exposed due to a reduction in vegetation growth. However, a few stretches of slow-moving water can be found close to the banks. At this time the snails are usually found deep in the stream mud or in the slack water. Between April and

August, the water flow is retarded by plant overgrowth from the banks. In August the stream can hardly be seen because of the overgrowth. The snails are found under rocks or on vegetation during this time. Throughout the year the land around the stream is used for grazing cattle and sheep, but they are usually present at the sampling site every three months so causing disturbance of the habitat.

Strain C was collected from a large boating pond at Llanfairfechan (SH 678754) close to the sea front. It has an inflow from the adjacent river, which mainly discharges straight into the sea. Between September and October the water level is quite high, approximately 1m, and the snails can easily be found browsing off algae around the pond wall or on plastic bags in the pond. Between the months of November and March the pond is extensively drained and only residual rainwater and sea spray is present. In these months the snails are found buried deep in the pond mud or where there is standing water. The pond is refilled in April for the summer months and sea trout and eels have been found during sampling.

Unlike the stream habitat of strain A, the pond is exposed and lacks any cover of vegetation. The only source of food is from the windblown leaves of nearby trees and benthic microalgae. Other animals that have been collected in the pond include gammarids, corixids and tubificids. The pond is drained each winter. However in August 1991, the pond had almost dried up due to the exceptionally prolonged hot weather.

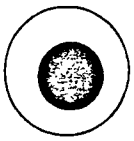
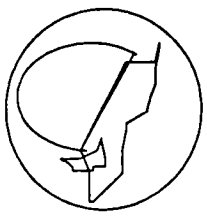
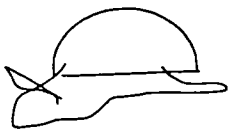
5.2 MATERIALS AND METHODS

5.21 Collection

Monthly collections of strain A and C snails were taken from September 1990 to September 1991. The snails were collected by throwing a 0.25m quadrat into the normal sampling area. The snails were either removed from stones with a fine paint brush, or the mud was dredged using a net and sifted to obtain the snails.

Table 5.1:

Maturity index developed to aid in the identification of the various stages of the embryos. Index is based on that shown in Hart and Begon (1982).

STAGE	DIAGRAM	DESCRIPTION
I		Small, white oocyte surrounded by a thin transparent gelatinous shell.
II		White embryo shows some form, but still does not look like a snail. Still surrounded by transparent shell.
III		Appears to resemble a juvenile snail. Starts to show some movement, but still encased in a shell.
IV		No longer surrounded by shell case. Has free movementand resembles juvenile snail.

5.22 Size Frequency

The shell length of the snails was measured using a binocular microscope (as described in chapter 2), and individuals were assigned to size classes ranging from 0.5mm up to a maximum of 5.5mm in increments of 0.5mm. Shell-length frequency histograms were used to show the relative distribution of size classes within each population throughout the year. Analysis of the distribution was achieved using probability paper to find which cohort was the most dominant.

5.23 Maturation

During each monthly collection adult snails had their operculum ently prized open to expose the embryos present in the brood pouch. As the embryos were at various stages of development, a maturity index (Table 5.1) was allocated to them based on Hart and Begon (1982) working on the reproductive strategy of winkles. The number of embryos present in each stage were counted and recorded.

5.3 RESULTS

5.31 Shell-length Frequency

strain A

Figure 5.1 shows the shell-length frequency histograms for strain A. Most of the months were examined using probability paper, which usually confirmed the trends observed in the histograms. Although juvenile and adults were present throughout most of the year, the samples were normally dominated by juveniles. In February and May 1991 no cohort was dominant. This was probably caused by the lack of recruitment of young in that month. July and August 1991 showed a shift towards the adults. In August no young were recruited. One explanation may be the overgrowth of vegetation around the stream, which lowered incident light and perhaps algal food supply. It was also a hot

Table 5.2A: Size-frequency distribution of strain A and C from September 1990 to September 1991.

A. STRAIN A

Month size (mm)	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APRI	MAY	JUN	JUL	AUG	SEP
0.5	12	15	1	0	0	0	30	20	10	5	0	0	18
1	20	42	65	28	9	0	17	15	17	26	0	3	25
1.5	48	41	158	6	23	7	125	63	38	80	36	12	69
2.0	44	58	86	3	24	50	92	70	45	116	34	27	58
2.5	32	20	25	3	15	26	75	36	27	49	22	34	45
3.0	6	14	20	1	9	43	43	11	22	21	9	13	14
3.5	7	22	17	0	7	18	18	16	25	21	67	68	14
4.0	12	39	14	0	14	22	21	20	21	21	47	100	14
4.5	25	19	20	0	19	36	32	15	29	27	54	112	28
5.0	29	1	1	0	0	26	8	0	0	0	3	26	54
5.5	2	0	0	0	0	0	0	0	0	0	0	1	2
TOTAL	237	271	407	41	120	228	462	266	234	366	272	396	341

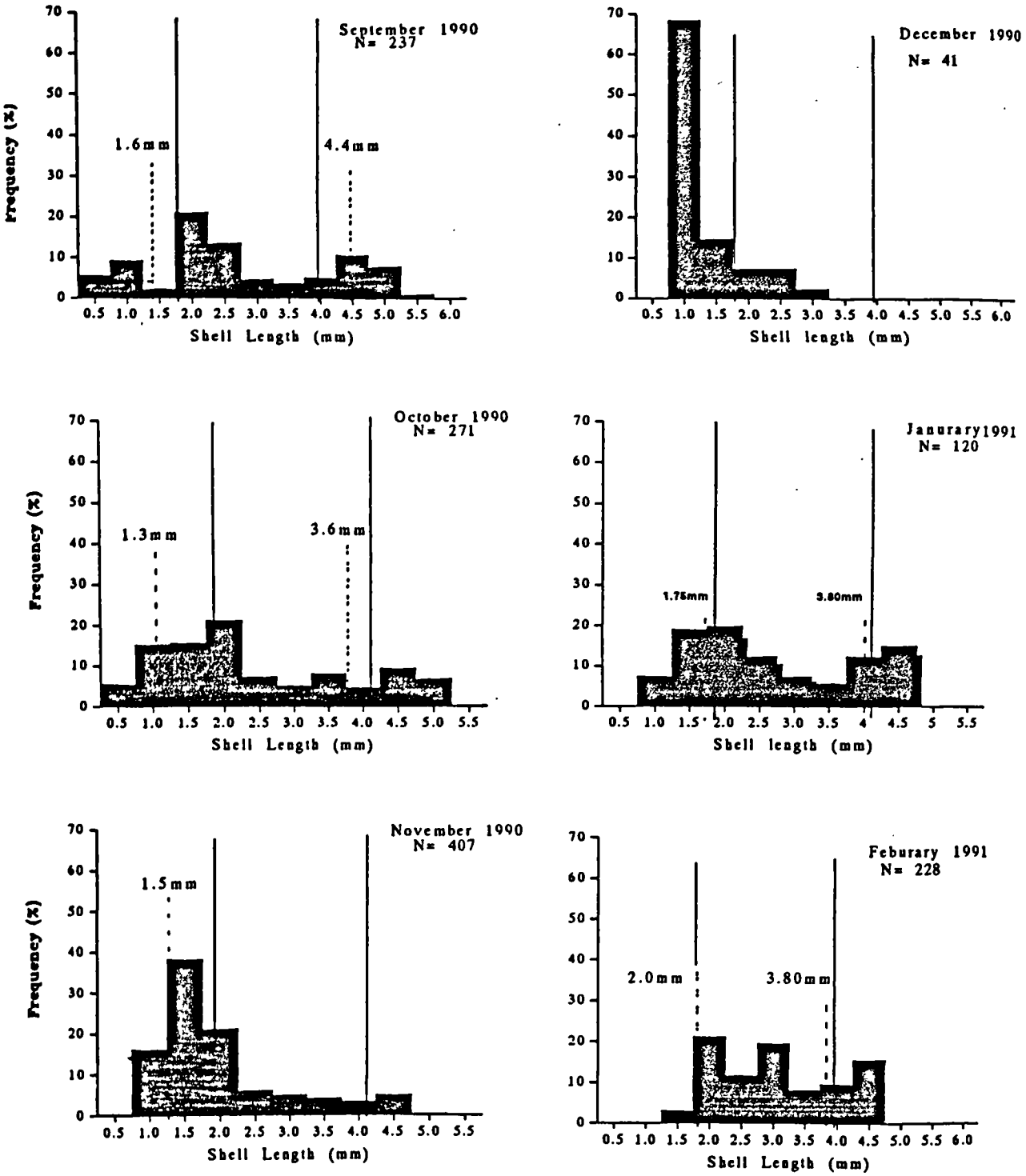
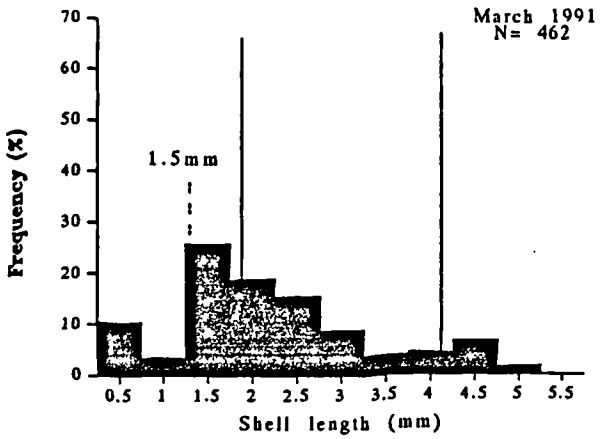
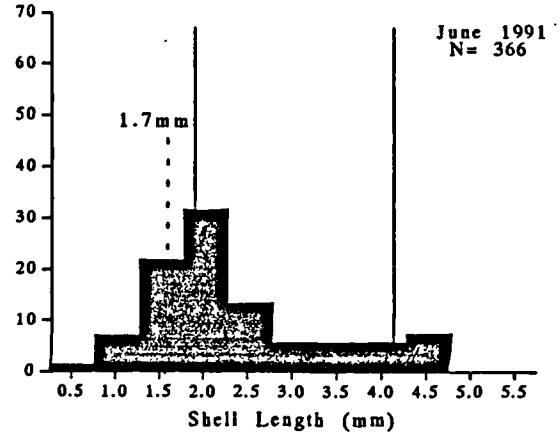
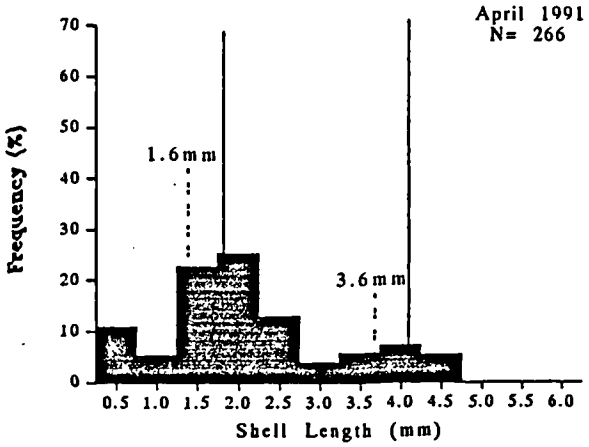
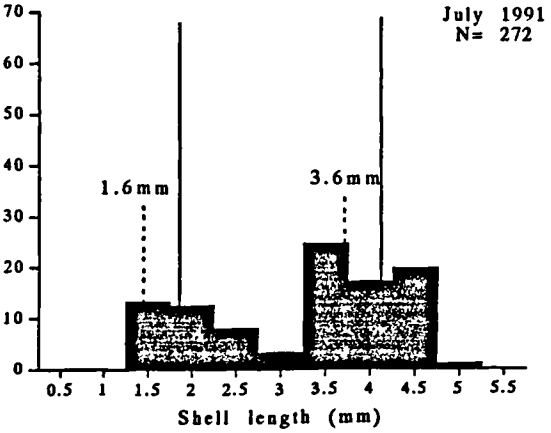


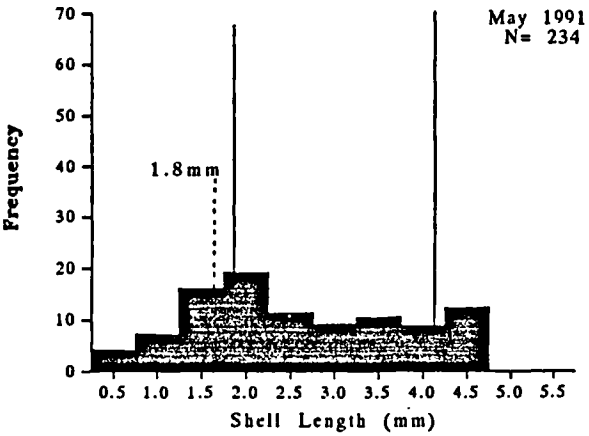
Figure 5.1: Monthly size-frequency distribution of strain A in its natural habitat. Sample sizes obtained each month are noted broken lines show mean size calculated using probability paper.

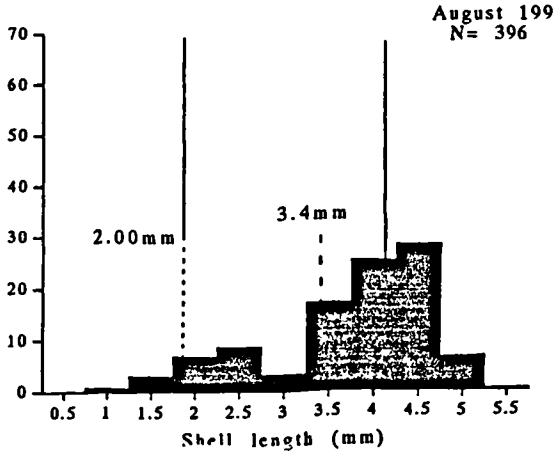

March 1991
N= 462
1.5mm
Frequency (%)
Shell length (mm)

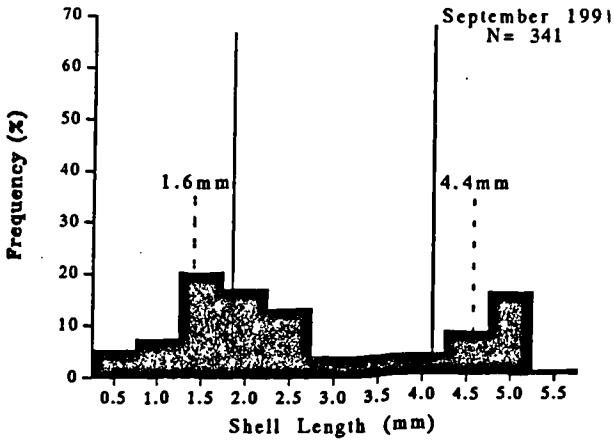

June 1991
N= 366
1.7mm
Shell Length (mm)


April 1991
N= 266
1.6mm
3.6mm
Frequency (%)
Shell Length (mm)


July 1991
N= 272
1.6mm
3.6mm
Shell length (mm)


May 1991
N= 234
1.8mm
Frequency
Shell Length (mm)


August 1991
N= 396
2.00mm
3.4mm
Shell length (mm)


September 1991
N= 341
1.6mm
4.4mm
Frequency (%)
Shell Length (mm)

summer and any young present may have died from desiccation.

Recruits in the September 1990 population showed rapid growth in October, but slowed their growth in November and would have died in December, but not before they could recruit any young. The young recruited in January showed slow growth until March. Only those recruited from March 1991 onwards showed rapid growth, which lasted up until September 1991.

Strain C

The monthly length-frequency histograms of the population of strain C are illustrated in Figure 5.2. As with strain A, the trends shown in the distribution confirmed that found with probability paper. Juvenile and adult cohorts were present throughout the year. December showed no distinct cohort, although the distribution was skewed towards the juveniles. By January adult and juvenile cohorts were present in equal numbers. February to April 1991 showed the juvenile size class to be the more dominant as young were possibly recruited to the spring population. May 1991 showed a dominance of adults, which recruited young to the June population. July and August showed one cohort to be dominant, large juveniles and this continued to September 1991, so that the adults dominated the population. In July and August the pond dried up due to the hot weather at the time. Any residual water present had high temperatures (27°C). This would have caused the young juveniles to die from heat stress or the adults may have ceased releasing young.

Recruits present in September 1990 showed fast growth from October through to November and died in December but did not appear to release any young. No significant recruitment was evident in December through to February 1991 due to the pond being drained. Recruitment began in March and continued to show a rise in April and May, but then declined in June such that by July and August no young were present. Recruitment recommenced in September 1991. It would thus appear that the autumn-winter population showed slower growth than the spring-summer population.

Table 5.2B:
B. STRAIN C

Month size (mm)	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APRI	MAY	JUN	JUL	AUG	SEP
0.5	11	52	9	12	0	0	7	19	11	7	2	0	15
1	9	26	56	17	48	2	21	6	2	25	6	0	14
1.5	14	15	54	7	17	30	107	48	7	47	4	3	16
2.0	39	37	74	22	31	73	47	54	22	64	47	3	45
2.5	40	45	48	13	13	37	34	24	22	80	84	141	31
3.0	32	18	24	2	11	19	22	18	15	43	100	129	43
3.5	64	46	58	0	25	32	44	28	17	35	32	79	66
4.0	79	95	54	0	38	23	23	17	48	61	48	29	405
4.5	22	16	9	0	9	8	6	3	30	22	12	7	27
5.0	0	0	0	0	1	0	0	1	0	1	1	0	0
5.5	0	0	0	0	0	0	0	0	0	0	0	1	0
TOTAL	310	350	386	73	193	224	311	218	174	385	336	427	662

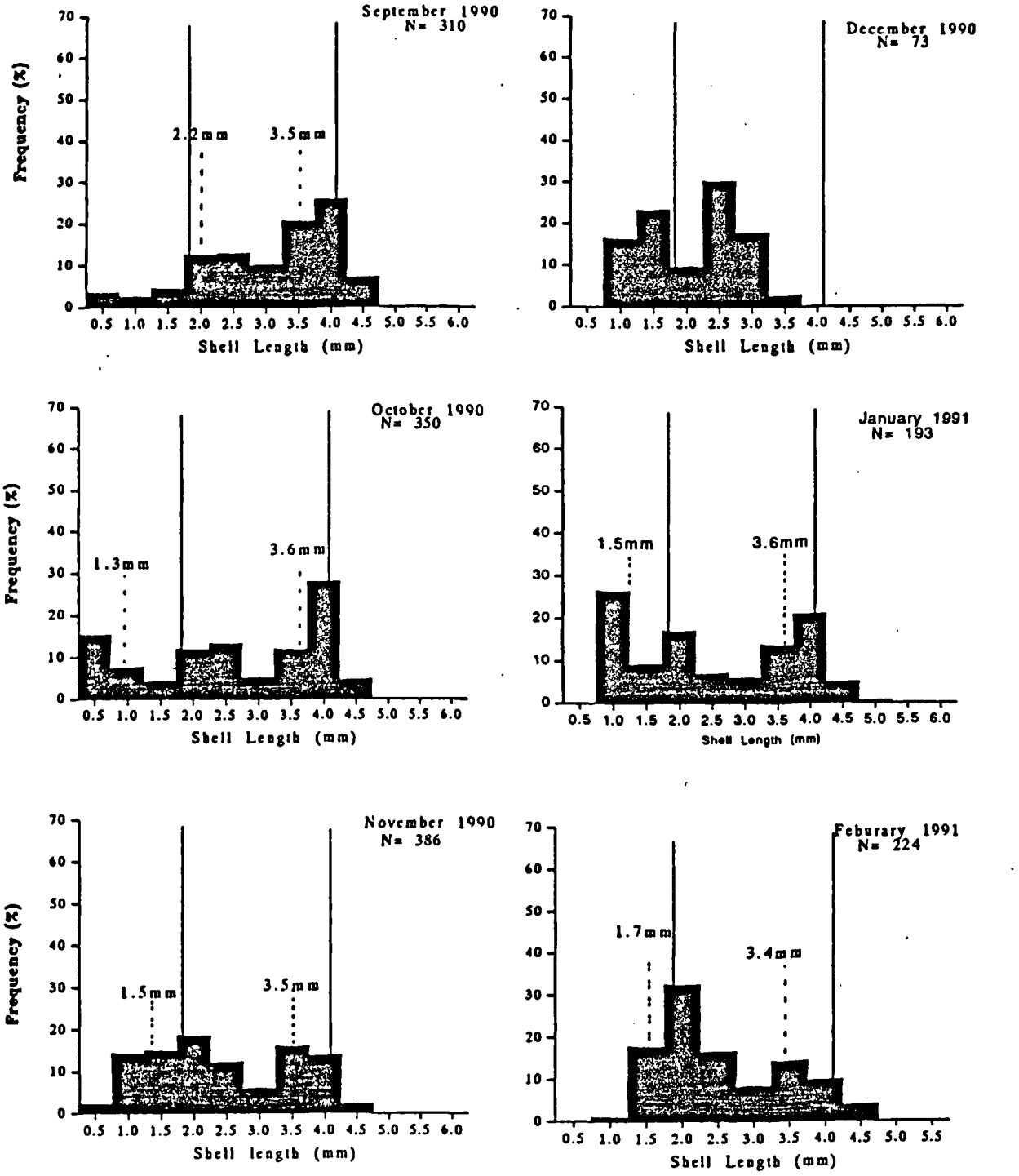
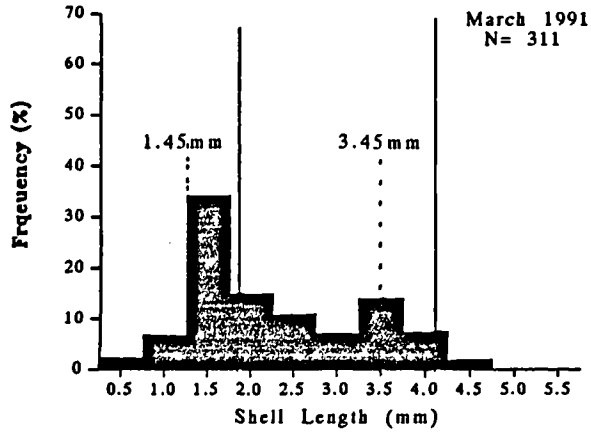
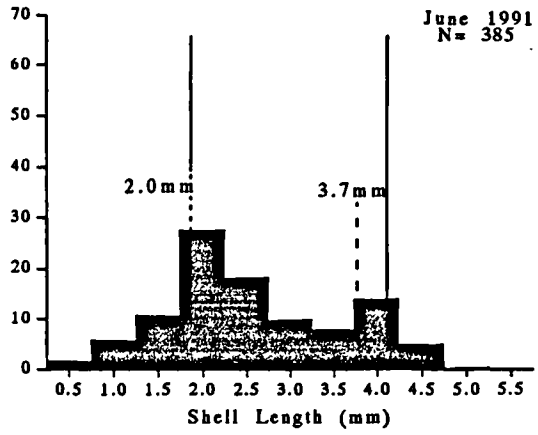
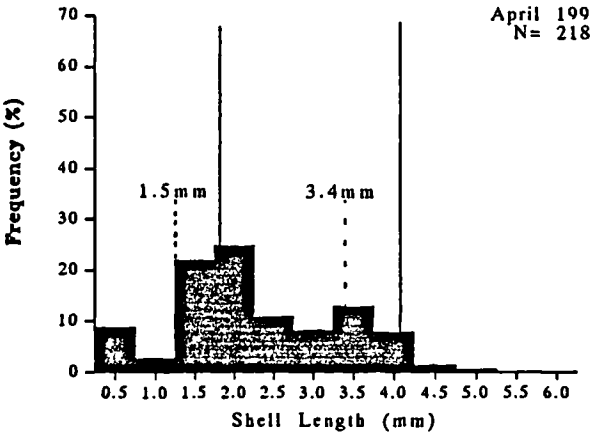
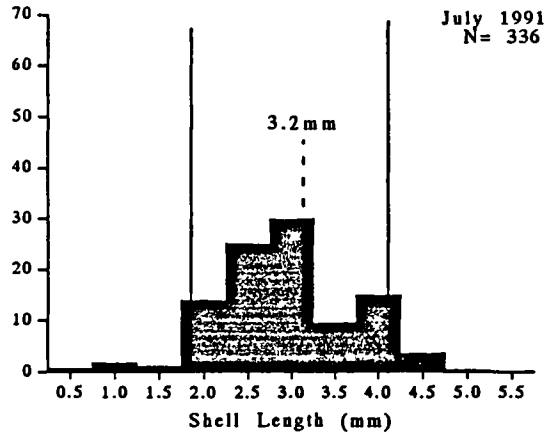


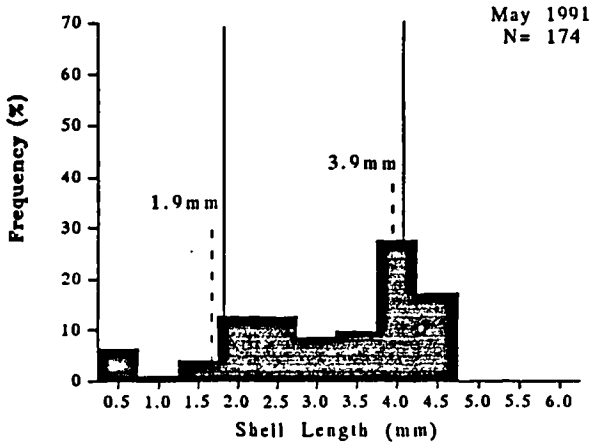
Figure 5.2: Monthly size-frequency distribution of strain C in its natural habitat. Sample sizes obtained each month are given, as is the dominant cohorts calculated each month using probability paper analysis.

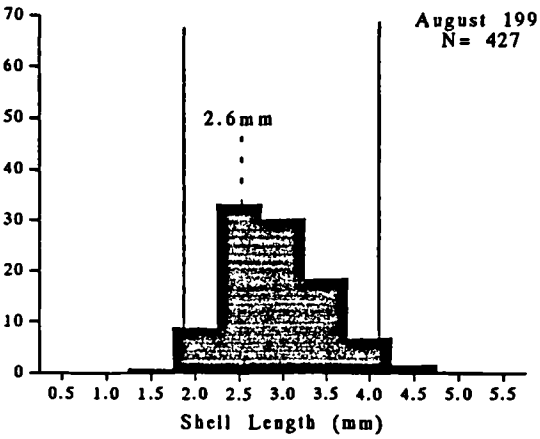

March 1991
N= 311
1.45mm
3.45mm
Frequency (%)
Shell Length (mm)

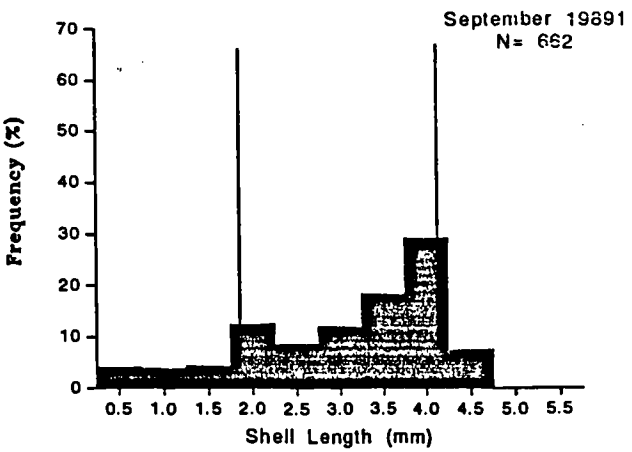

June 1991
N= 385
2.0mm
3.7mm
Shell Length (mm)


April 1991
N= 218
1.5mm
3.4mm
Frequency (%)
Shell Length (mm)


July 1991
N= 336
3.2mm
Shell Length (mm)


May 1991
N= 174
1.9mm
3.9mm
Frequency (%)
Shell Length (mm)


August 1991
N= 427
2.6mm
Shell Length (mm)


September 19891
N= 662
Frequency (%)
Shell Length (mm)

5.32 Reproductive activity

Figures 5.3a and 5.3b show the distribution of the embryonic stages each month in the two strains. Strain C appeared to show periodicity at all its embryonic stages (Figure 5.3b). This was reflected in the number of embryos ready for release (Figure 5.4), showing peaks in November, February and June (Fig. 5.4). After each of these months there was a drop in the percentage of embryos ready for release. Those sharp drops correlated well to the recruitment shown in shell-length frequency histograms (Fig. 5.2). The periodicity shown in the strain C population could result from environmental pressures owing to the pond being drained and the environment being exposed to wind, spray and presumably wide temperature fluctuations.

Strain A showed little periodicity during its embryonic stages of development (figure 5.3a) and the population maintained a fairly constant high level of embryos ready for release (figure 5.4). There appeared to be no seasonal or environmental influence on reproductive development. The only time strain A showed a drop in the percentage of stage IV embryos (Figure 5.4) was between April and August, when the stream was heavily choked with vegetation.

5.4 DISCUSSION

Strain A showed continuous recruitment of young throughout most of the year. Constant recruitment of young was possible because in each month there were individuals of 4.5mm or more, at which length strain A snails become sexually mature (chapter 2). This continual recruitment of young agrees with the size-frequency distribution patterns found by Dussart (1977).

Strain C snails matured at between 3.5mm and 4mm. As individuals of this size range were present in nearly all months, the population should have been capable of continually releasing young . The absence of young in the samples collected in December

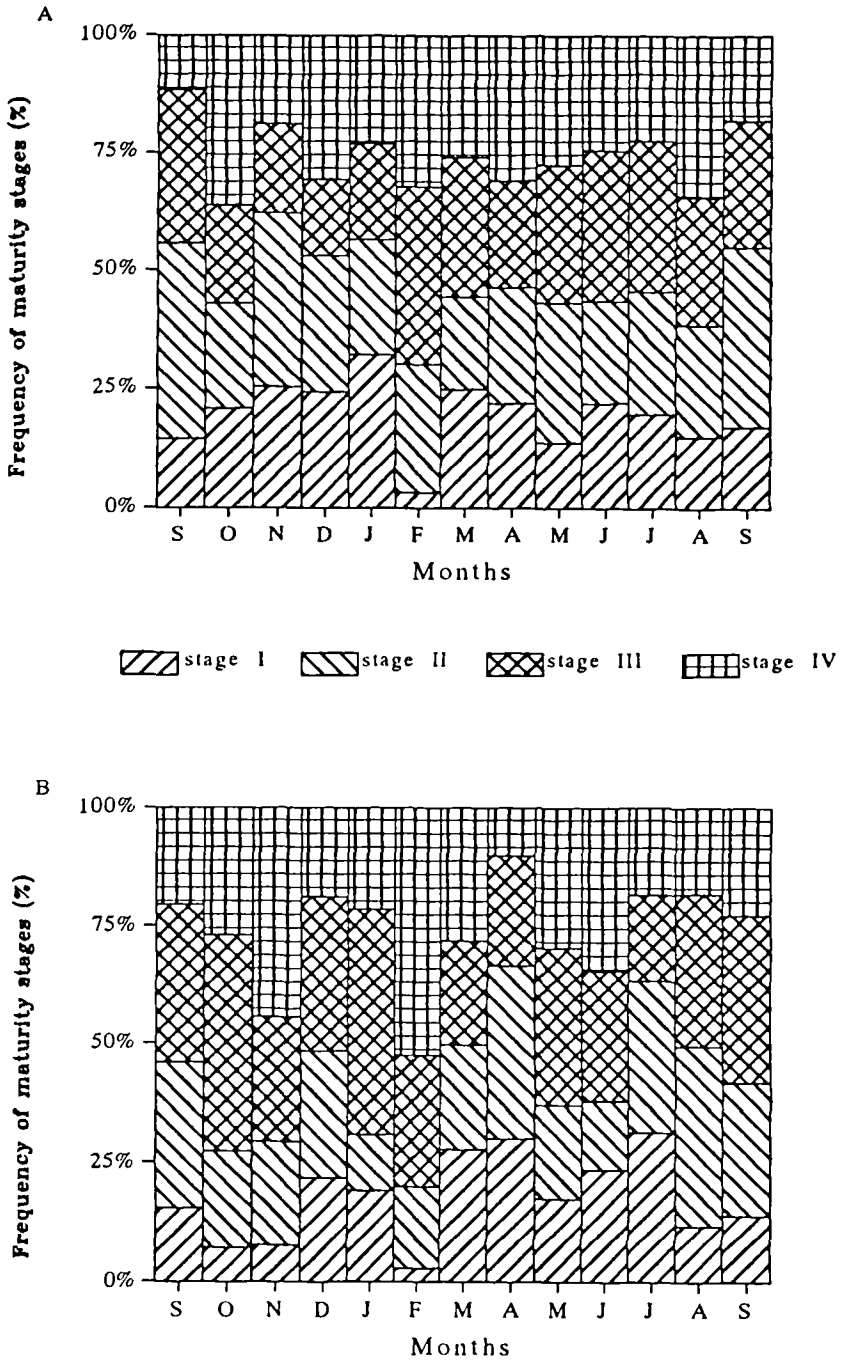


Figure 5.3: The reproductive cycle of (A) strain A and (B) strain C, based on the proportion of the population at various maturity stages (see Table 5.1).

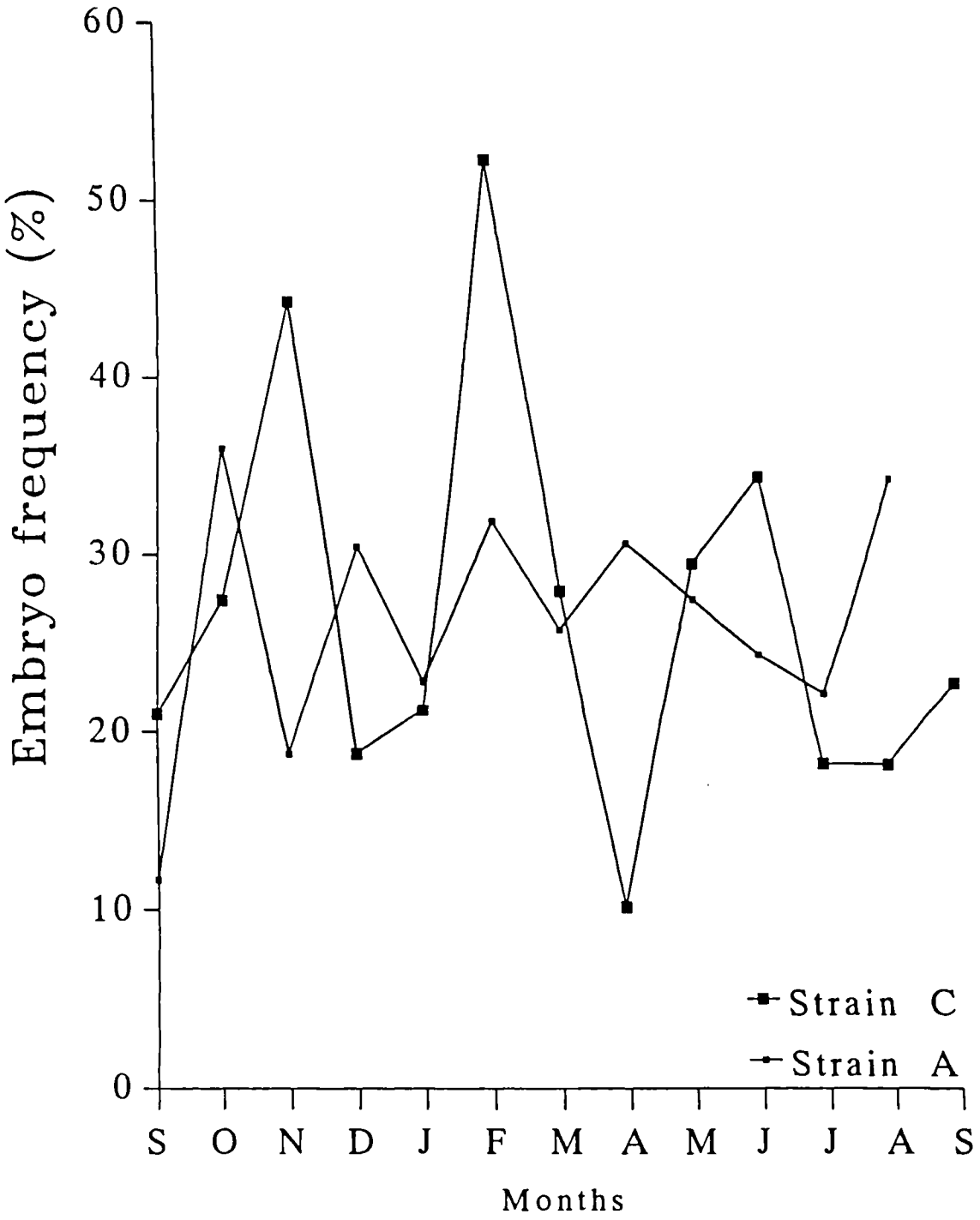


Figure 5.4:
Monthly percentages of embryos (stage IV) ready for release in strain A and C adults during September 1990-September 1991.

to February and July to August were most probably due to the environmental pressures experienced in those time periods. The results suggest the life span of strain A and C to be approximately three months, as found by Winterbourn (1970), and that there were five generations in the one year, with a break in recruitment between the months of December and February.

The two strains showed differences in their size distributions throughout the year. The strain C population was dominated by small adults and many juveniles, whereas the strain A population was dominated by large adults and fewer juveniles. In the same months that recruits dominated the strain A population, adults dominated the strain C population. In most months the strain C population was shown to have distinct cohorts and was easier to interpret than strain A population.

The relatively high abundance of juveniles in the strain A population could have been due higher mortality, as shown in the laboratory (chapter 2) and in order to compensate for this, strain A adults release many young. The mortality in the field could have perhaps been partly attributable to predation by leeches (Young and Ironmonger, 1979; Young and Proctor, 1986), which are abundant in their habitat.

The relatively high abundance of small adults in the strain C population may have reflected the environmental harshness of their habitat. This environment is unpredictable. Changes may occur in the level of food availability and the environment is exposed to climatic conditions. In order to take full advantage of the transiently favourable conditions, it is necessary for the snails to show early maturation and release young to start a new generation. This earliness in maturation was also shown in the laboratory when snails were reared from birth (chapter 2).

Evident in most months was the simultaneous presence of at least two generations in both the strain A and C population. Dussart (1977), studied the ecology of *Potamopyrgus jenkinsi* in the North West of England, where he found that at eleven sites two generations were present in each month, as was shown in the present study. The strain C population showed a single peak once, in August 1991. At that time the pond

water had dried up due to the prolonged hot weather. Where water was present the temperature ranged from 17^0 C at the inflow to 27^0 C in the shallow pool of standing water. Probably the juveniles were not able to cope with high temperatures and desiccation as effectively as the larger adults. Also, no recruitment of young took place in that month.

Both strains appeared to have a life span of 3 months, which agrees with Frömming (1956). Dussart (1977) failed to observe such a reproductive pattern, but his did agree with Michaut (1968) continuous reproduction throughout the year. Boycott (1936) suggested an annual cycle, previously having observed that some snails could survive for two years (Boycott, 1929). When the two strains were reared under constant conditions in the present study (chapter 2), some snails survived for over 12 months.

Strain C showed periodicity in its embryo production and subsequent release of young while strain A showed constant reproductive activity. This difference could be a environmentally induced (see above). Thus strain C shows opportunistic tendencies in its embryo production and population recruitment, accumulating embryos during harsh conditions and releasing the young in more favourable conditions. Such opportunistic behaviour has been seen in other molluscs (e.g. Hornbach *et al.*, 1980; and Etter, 1989). Hannaford Ellis (1983) found seasonal reproductive periodicity in *Littorina nigrolineata* and *L.neglecta*. This could have been caused by high mortality rates in adults. Alternatively it could have been due to heavy investment in reproduction. In the former the result is high investment in reproduction early on in the life history. The result of the latter is death to the parent. In comparison with that of strain C, the environment of strain A is stable and abundant in food. So here it may be advantageous to delay reproduction until the adult reaches a larger size, with a concomitantly larger lifetime fecundity. The only time strain A failed to recruit young was in July and August, which correlates with the dense overgrowth of vegetation at that time. Embryo production continued despite there being no recruitment of young. The embryos were accumulated in the reproductive

tract, ready to be released under more favourable conditions.

It would appear that the life histories shown by the two strains have similar characteristics to those proposed in 'r' and 'K' selection (Pianka, 1970). Strain C approximates to an 'r'-selected organism in that it has unstable population dynamics, shows early maturation and has a high reproductive effort. Strain A approximates to a 'K'-selected organism as its population dynamics are more stable, individuals have slower growth, become larger as adults and show less reproductive effort.

Differences in life-history characteristics exhibited in the field also persisted under constant laboratory conditions (see chapter 2). Although strain C showed no reproductive periodicity under constant conditions, it still released young at an earlier age and size than strain A. It would appear that the habitats of the two strains produced different selection pressures. These genetically based differences in life-history characteristics interact with phenotypically plastic responses to the environment to shape the overall population dynamics. The phenotypic response is most obvious in the reproductive periodicity of strain C.

CHAPTER 6:

GENERAL DISCUSSION

Organisms may alleviate the effects of environmental variability through a range of physiological, morphological and behavioral modifications. Natural selection has favoured four basic responses for adjusting phenotypes to environmental heterogeneity (Mayr, 1963; Levins, 1968). Individuals may 1) express a constant phenotype independent of the environment (homeostasis or canalisation), 2) produce a flexible phenotype adjusted by selected features of the environment (plasticity), 3) have genetically based, environmentally induced developmental switches (developmental conversion) or 4) differ genetically with respect to a particular trait (genetic polymorphism). The strategy favoured by natural selection depends on the character involved and the nature and scale of environmental heterogeneity (Levins, 1968; Roughgarden, 1972).

Because *Potamopyrgus jenkinsi* is an apomictic parthenogen, its offspring will be identical to the parent. In the absence of mixis, rapid selection of new genotypes is impossible, so in order to survive changes in the environment from one generation to the next, other mechanisms need to be adopted. Jaenike and Selander (1979) suggested that clones surviving in the long term must be able to cope with environmental changes by having robust phenotypes. Their physiology and development should be flexible and their habitat broadly-niched. These characteristics should be programmed by a "general-purpose-genotype" (Baker, 1965).

The present study measured the life-history parameters of growth, fecundity and survival in the two morphological strains A and C of *Potamopyrgus jenkinsi*. The preceding chapters fully discuss the results of rearing snails from these strains under constant laboratory conditions. This includes the response of newly released juveniles, older juveniles and adults to manipulated food ration and salinity. The important outcome was that the above traits differed between the two strains, both under constant, and manipulated conditions. This difference may have a genetic basis. The present chapter discusses whether one of the two strains is better adapted to changing environments,

whether such adaptation is related to characteristics of the native habitat, and the possible basis of co-existence in certain habitats. Ecological-genetical studies by Johnson (1981), in relation to the habitat of several species of *Hydrobia* and strains A and B of *Potamopyrgus jenkinsi*, found that while strain A was a 'generalist' in relation to other freshwater animals, it was a 'specialist' with regards to the *Hydrobia* species.

6.1 TRADE-OFFS

Trade-offs are central to the development of life-history theory (Bell and Koufopanou, 1986; Stearns, 1989a). Usually, the physiological trade-off between fecundity and survival is considered. An increase in current reproductive investment is assumed to cause a decrease in longevity and in future reproductive effort. This has been termed the "cost of reproduction" (Stearns, 1976). This may also play an important role in determining the relationship between growth and reproductive success (Stearns, 1976), with extra investment in offspring occurring at the expense of somatic growth (Berger, 1989; Green and Rothstein, 1991).

The present study measured reproductive investment as the number of young released. The two strains, when reared in optimal conditions, showed no trade-off between fecundity and survival. A similar lack of correlation was found by Bell (1984) in cladocerans. Instead, a trade-off was found between reproductive effort and somatic growth, which is also explained by life-history theory (Gadgil and Bossert, 1970). In the present case, when the environment was manipulated (e.g. food ration), the two strains differed in their reproductive effort. Strain A reduced or ceased releasing young but maintained higher survivorship, whereas strain C continued to release young, albeit at a reduced rate, to the cost of survivorship. The reproductive response of strain A therefore appears to be more sensitive to environmental cues. This may account for its ability to colonize and exclude strain C from more habitats.

The following conclusions can be drawn. Under environmental stress reproduction has a negative effect on survivorship and the quantitative differences in this trade-off between strains A and C suggest that phenotypic plasticity in reproductive behaviour is an important life-history trait in these snails.

6.4 GENOTYPE-BY-ENVIRONMENT INTERACTIONS

In young snails there is no significant genotype x environment interaction which would indicate the strains to differ in their response to environmental changes. In fact at this stage of their life history the strains show no variation in genetically determined trait (Table 6.1). Only the environment causes the greatest variation among the snails. However, by the next stage of their development (large juveniles) there is a significant genotype x environment interaction. This indicates that the strains start to differ in their response to the environment. In the starvation and food ration experiment, the effect of strain as well as treatment is significant. However, it is the strain effect that accounts for most of the variation, therefore showing the genotype to have the greater effect. But, when salinity is altered, it is the environment which has the greater effect.

The adults also showed significant genotype x environment interactions, in the starvation and salinity experiment. The interaction in the starvation experiment was significant while that in the food ration was not. In both these cases the effect of strain was not significant. A possible explaination for the difference in results is the two extreme feeding regime in the starvation experiment, whereas in the food ration experiment dealing also with intermediary food levels and so the genotypic effect may be less pronounced. However, in increased salinity it is the genotype that causes the greatest amount of variation.

Table 6.1: Summary of the main effects and interaction between the two strains when the environment was manipulated. A sinificant result is represented by a +, a non significant result is represented by a x. The strain that showed the greatest survivorship in each of the test environments is listed as well as the environemnt, written in the brackets.

STARVATION EXPT

size class	STRAIN	TREATMENT	STRAIN xTREAT	GREATER SURVIVORSHIP
newly released juveniles	X	+	X	Strain C (Fed and starved)
large juveniles	+	+	+	Strain A (Fed and starved)
adults	X	+	+	Strain C (Fed and starved)

FOOD RATION EXPERIMENT

size class	STRAIN	TREATMENT	STRAIN xTREAT	
newly released juveniles	X	X	X	Strain A, (High) Strain C, (Low + Starved)
large juveniles	+	+	+	Strain A, (Starved) Strain C, (High, Med, Low)
adults	X	X	X	Strain A (Starved) Strain C (High, Med, Low)

SALINITY EXPERIMENT

size class	STRAIN	TREATMENT	STRAIN xTREAT	GREATER SURVIVORSHIP
newly released juveniles	X	+	X	Strain A, (in all)
large juveniles	X	+	+	Strain A, (5%SW) Strain C, (0%, + 20%SW)
adults	+	+	+	Same

Thus the strains begin to differ when they are large juveniles and this continues into adulthood. But in restricted food availability the genotypic differences occur early, whereas in increased salinity genotypic differences are only pronounced when the snails are adults. This may be important, for depending on which stage the strains have reached in their life history when environmental change occurs, may be critical in determining whether one may out-compete the other or vice versa.

6.2 PHENOTYPIC PLASTICITY

Natural selection acts on the genotype via the phenotype (Stearns, 1989b; Rice and Mack, 1991). Phenotypic plasticity is the degree to which the phenotype, associated with each genotype, varies in response to environmental change as, for example, expressed in a reaction norm (Woltereck cited in Stearns, 1989b; Stearns *et al.*, 1991).

If plasticity is present, the individual phenotype will be modified by the degree of variability in the environment. Caswell (1983) argued that plasticity is irrelevant in a uniform environment. In the present study, however, the life-history traits of growth, fecundity and survival of the two strains differed significantly under optimal conditions. Electrophoretic studies by Johnson (1981) and DNA fingerprinting by Hauser *et al.* (1992) found the strains to have different genotypes, each stable between generations. Therefore the differences seen in the above life-history parameters are probably explicable at the level of the genotype.

In a variable environment, natural selection acts on the entire reaction norm and not on one point of it (Stearns, 1989a). The two strains are plastic under the variable experimental conditions used and adjust their phenotypic traits (e.g. growth) accordingly to the environmental effect. They differ in the degree of their plasticity, as demonstrated by the significant genotype-by-environment interaction, strain C faring better at low food

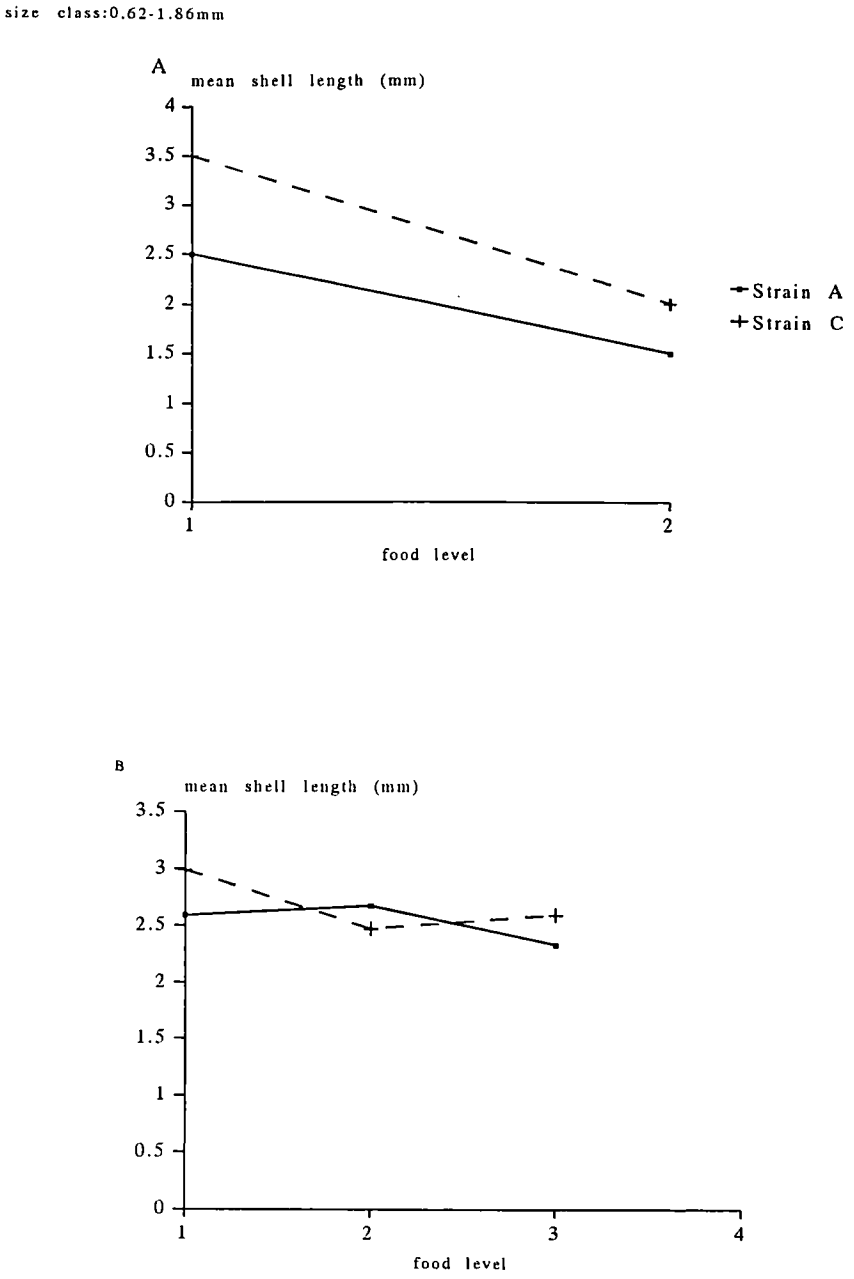


Figure 6.1: Reaction norms of strain A and C large juveniles when food is A) present or absent and B) rationed. Food level 1 and 2 is fed and starved, respectively for for graph A. For graph (B), food 1,2,3 and 4 are high, medium, low and starved respectively.

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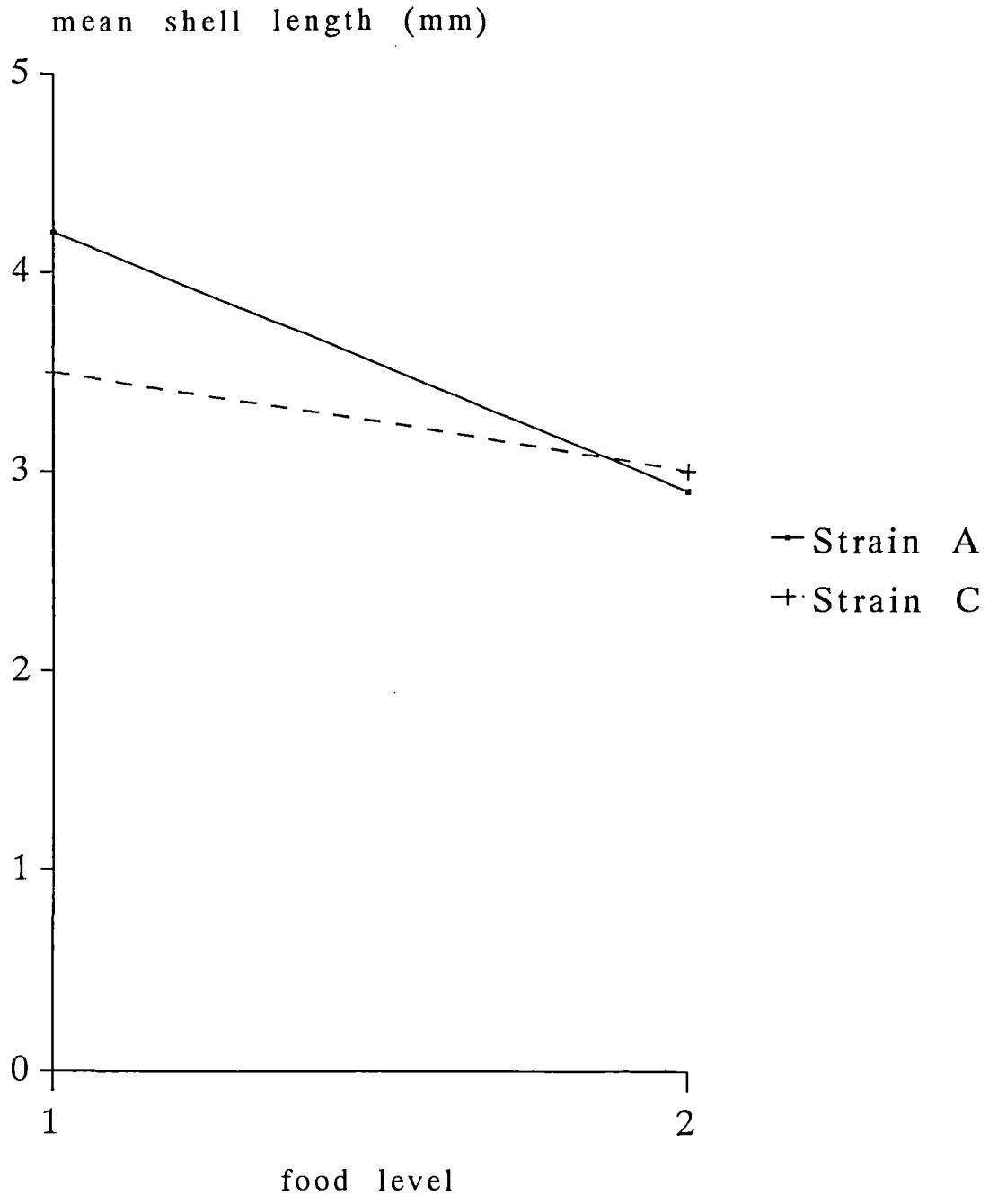


Figure 6.2: Reaction norms for strain A and C adults in in (1) fed and (2) starved environments. Points are are mean values at the end of the experiment. Broken and solid lines represent possible norms of reaction.

ration and higher salinity than strain A.

The reaction norms for juveniles when food is either present or absent (Fig. 6.1a) show strain C performing and showing the greater response than strain A under both conditions. Over a range of food rations, the reaction norms cross (Fig. 6.1b), again showing strain C performing better than A in good and poor feeding conditions. For adults, the reaction norms cross (Fig. 6.2). A marked, genotype-specific response to environmental change will result in a wider ecological distribution of the phenotype than would be seen in a population composed predominantly of a less responsive genotype (Thompson, 1991). The adults of strain A seem to conform to the former and those of strain C to the latter. Thus in the adults, strain A is the more plastic, showing the greater response to environmental variation. However, strain A is also well adapted to good feeding conditions, just as strain C is adapted, to a lesser extent, to poor feeding conditions.

The two strains used in this study are both from spatially different environments. The strain C population inhabits an unpredictable environment whose salinity and water volume vary as the pond is drained and refilled seasonally. The strain A population, on the other hand, is from a more predictable, inland-stream environment. However, as stated in chapter 1, strain A is known to exist in certain brackish habitats (Warwick, 1952; Winterbourn, 1970; Johnson, 1981), although strain C is generally not present in inland waters, typically occupied by strain A.

Because of the unpredictable environment of strain C it means it is necessary for the snails to mature early at a relatively small size and release young while conditions are still favourable. The young that are released in poor-feeding and high-salinity conditions when the environment is deteriorating, may be better able to withstand those conditions than the adults and so may be the sole representatives of the population when benign conditions return. Strain A, on the other hand, shows superior growth and fecundity to strain C in favourable conditions. However, its release of young ceases when conditions become unfavourable. Although this trait may exclude strain A from areas of poor food

supply and high salinity, it could be beneficial to the strain in many freshwater habitats. Halting the release of young can enable the adults to either disperse to areas high in resources or wait until conditions become favourable. Thus, when finally released, the young will have improved prospects for growth.

The superior performance of strain C in poorer environments suggests that it may adopt a "bet-hedging" strategy of resource allocation. Bet-hedging theory was originally formulated by Gillespie (1974) and Slatkin (1974) and concerns the trade-off between the mean and variance of fitness (Philippe and Seger, 1989). If there are two phenotypes, one may do better than the other in good conditions and worse in poor conditions. The second phenotype may not do as well in good conditions as the first phenotype but in poor conditions, although it does badly, it is still better than the first phenotype.

Is this Plasticity adaptive?

Plasticity is adaptive if associated fitness is maintained at a high level relative to that of other genotypes, and this may be achieved by either variation or stability of the phenotype or both (Stearns, 1989a; Lessells, 1991; Thompson, 1991).

Genetic variation and phenotypic plasticity have been treated theoretically as alternative adaptive strategies to variable environments (Lewontin, 1957; Levins, 1968). In the present study, both strains of *Potamopyrgus jenkinsi* are plastic to differing environments, which suggests them to be adaptive. Moreover, under optimal conditions the strategies adopted are still different which suggest them to be genetically determined. Indeed recent work (Caswell, 1983; Via and Lande, 1985; Stearns and Koella, 1986) has clearly shown plasticity to have a genetic basis and can evolve in response to selection.

The problem that usually exists in estimating physiological trade-offs is separating the contingent (phenotypic) from the evolved (genotypic) responses (Møller *et al.*, 1989b). In the present study, the individuals of each strain are identical to the parent and so the ability of the two strains to persist over a wide range of physiologically diverse environments may result from a "general-purpose genotype".

6.3 GENERAL-PURPOSE GENOTYPE

A general-purpose genotype is defined as one which is ecologically broad-niched and physiologically and developmentally flexible (Baker, 1965). Johnson (1981), from electrophoretic studies, found strains A and B to be monomorphic (ie, all individuals have the same phenotype) and highly heterozygous. Thus their populations may have a greater capacity to exploit the whole resource spectrum than comparable mictic lineages, as suggested by Van Valen (1965) and Roughgarden (1972).

The two strains, A and C, in this study, with their ability to be plastic over a wide range of conditions, seem to show a general-purpose genotype. However, the fact that strain C snails can still release young in poor-feeding and high-salinity conditions where strain A cannot, suggests that strain C is the more generalized and strain A the more specialized. This is in agreement with Johnson (1981), who suggested strain A to be relatively specialized among several hydrobiid species.

6.5 RELATION TO HABITAT

Adaptation of the two strains to varying feeding and salinity conditions has now been quantified (chapters 3 and 4). But how does this information relate to their natural habitat? Caswell (1983) maintained that spatial variation can generate differences between individuals based on their location during development.

A stream at Criccieth, where snails were obtained for electrophoretic studies (appendix 1), flowing directly into the sea, contained both strains A and C. Although not present in large numbers, the two strains appeared to occupy ecologically distinct habitats. Strain A present exclusively upstream and strain C close to the confluence with the sea. Jaenike and Selander (1979) argued that in order for parthenogenetic organisms

to co-exist, they should not all have general-purpose genotypes, as this would cause them to experience intense competition. Vrijenhoek (1979), on the other hand, asserted that a clear line could not be drawn between generalism and specialism: i.e. broad ecological tolerance shown in one axis (e.g. food resources) does not necessarily imply the same for all axes (e.g. temperature). He suggested instead that co-existing clones must have different fecundity and survivorship patterns, as shown by strains A and C in this work.

Ecological separation of the strains has been suggested by Warwick (1952). Strain A is typical of freshwater and strains B and C are typical of coastal waters. Hylleberg (1975) argued from experimental evidence that unpredictable, heterogeneous environments would allow the co-existence of hydrobiid species if each performed better at different times and places. He concluded that under stable and predictable environments one species would be overwhelmingly successful through competitive exclusion.

Clonal populations, such as those of strain A and C, show only very slight ecological differences ("character displacement" *sensu* Fenchel, 1975) and so competition may result in the exclusion of one strain. This may occur with regards to strain C. Although physiologically able to occupy strain A habitat, strain C is not usually present there. Where co-existence does occur, as in the Criccieth stream, the two strains adopt distinct habitats. Thus, strain A is excluded from strain C habitat, as physiologically it is unable to cope with the high salinities, while strain C is excluded from strain A habitat probably by intense competition. A similar case is shown with respect to strain B being competitively excluded by strain A (Johnson, 1981).

6.6 CONCLUSION

The success of *Potamopyrgus jenkinsi* in colonising most of Britain and Europe is probably due to the phenotypic plasticity, shown by strains A and C in the present study. Clear differences have been demonstrated in their fitness (as indicated by the intrinsic rate of population increase calculated from life tables), ecology and life-history strategies. Both strains possess a "general-purpose genotype", but strain C appears to be the more opportunistic generalist (more of a "fugitive" or "weedy" phenotype) while strains A is the more specialized.

6.7 FURTHER RESEARCH

The present study has concerned itself with just the two strains A and C. Ideally, the same rearing and environmental manipulations should be repeated but including all three strains (A, B and C).

Mentioned above is the possible competition between the strains. This would be interesting to study as it has been suggested (Johnson, 1981; present chapter) that strain A may prevent subsequent invasion of the other two strains and so perhaps explain why strain A has monopolised freshwater systems. Competition experiments should simulate poor environmental conditions and use the same number of snails for each strain, as density may differentially affect life-history parameters of the strains. Ideally, a comparison should between strains derived from the same water system and between strains from spatially different habitats. Biochemical analysis of energy reserves might reveal whether the strains differ in their allocation of resources under environmental stress. In all cases, the experiments ideally should take place in the laboratory as well as in the field.

APPENDIX 1:

ELECTROPHORETIC STUDIES ON *POTAMOPYRGUS JENKINSI*

INTRODUCTION

A major concern of population genetics is the distribution of alleles at different loci within and among populations (Jarne and Delay, 1991). Such differences have extensively been investigated with the use of gel electrophoresis (e.g. Ward and Warwick, 1980; Janson and Ward, 1984; Heller and Dempster, 1991; Beaumont *et al.*, 1988), a powerful technique that allows quantifiable analysis of genetic differentiation.

ELECTROPHORESIS

Electrophoresis works on the principle that, except at their isoelectric point, proteins can either carry a net positive or negative charge (determined by their amino acid composition and the pH of the medium). When a uniform electric field is applied across the gel, the proteins migrate out at different speeds. Any allelic differences (different forms of a gene) that may occur at a protein-coding locus, that result in changes in net charge can thus be identified.

In the process of electrophoresis, a gel, usually made out of starch or polyacrylamide, has a sample applied to it. A direct current is conducted through the gel for normally 3-5 hours. The length of time usually depends on composition of the buffer solution used to make the gel, its ionic strength and the thickness of the gel. The proteins within the sample move in a direction determined by the sign of their net charge at a rate proportional to the magnitude of that charge. The rate of migration is also influenced by the size and configuration of the protein.

The final result of the electrophoretic procedure is a series of bands, revealed by several staining techniques, which identify the location of various forms of a single protein on the gel. Specific staining for enzyme activity allows particular isozymes to be determined at one time. Thus the banding pattern gives information on an individual's

genotype with respect to the locus (loci) coding for that particular protein. The staining methods used are normally chromogenic or fluorogenic techniques used in electron-transfer dye systems (Harris and Hopkinson,1976).

The characterization of an enzyme's electrophoretic activity on a gel is called the isozyme method (Utter *et al.*, 1984). "Isozyme" refers to an enzyme which differs in its electrophoretic mobility, but shares the same substrate or reaction with another (Markert and Moller, 1959). "Allozyme" (Prakash *et al.*, 1969) refers to the electrophoretic expression of allelic proteins at a particular locus. Whereas the activity of allozymes can differ among individuals, the banding patterns that represent the protein structures, based on the genetic code, should remain constant.

INTERPRETATION OF BANDING PATTERNS ON GELS

The banding patterns produced are phenotypic expressions of the genotype (alleles). Because the *in vitro* environment hardly influences the protein's structure, the genotypes can be deduced from the phenotype when the subunit composition of the protein is known.

Enzymes are composed of either one (monomeric) or several (multimeric) sub-units. In an isozyme these sub-units can be identical (homomeric) or different (heteromeric). Indeed the banding patterns on the gels after electrophoresis depend on the number of sub-units present. The simplest is a monomeric protein which is composed of single sub-units (i.e. a single polypeptide chain). More complicated banding patterns are produced when the active protein is multimeric (i.e. composed of two or more sub-units). Typical banding patterns produced by monomers, dimers and tetramers are shown in Figure 1. In all cases the homomeric isozymes are shown in homozygote individuals and heteromeric isozymes in heterozygotes. The banding patterns produced by heterozygotes

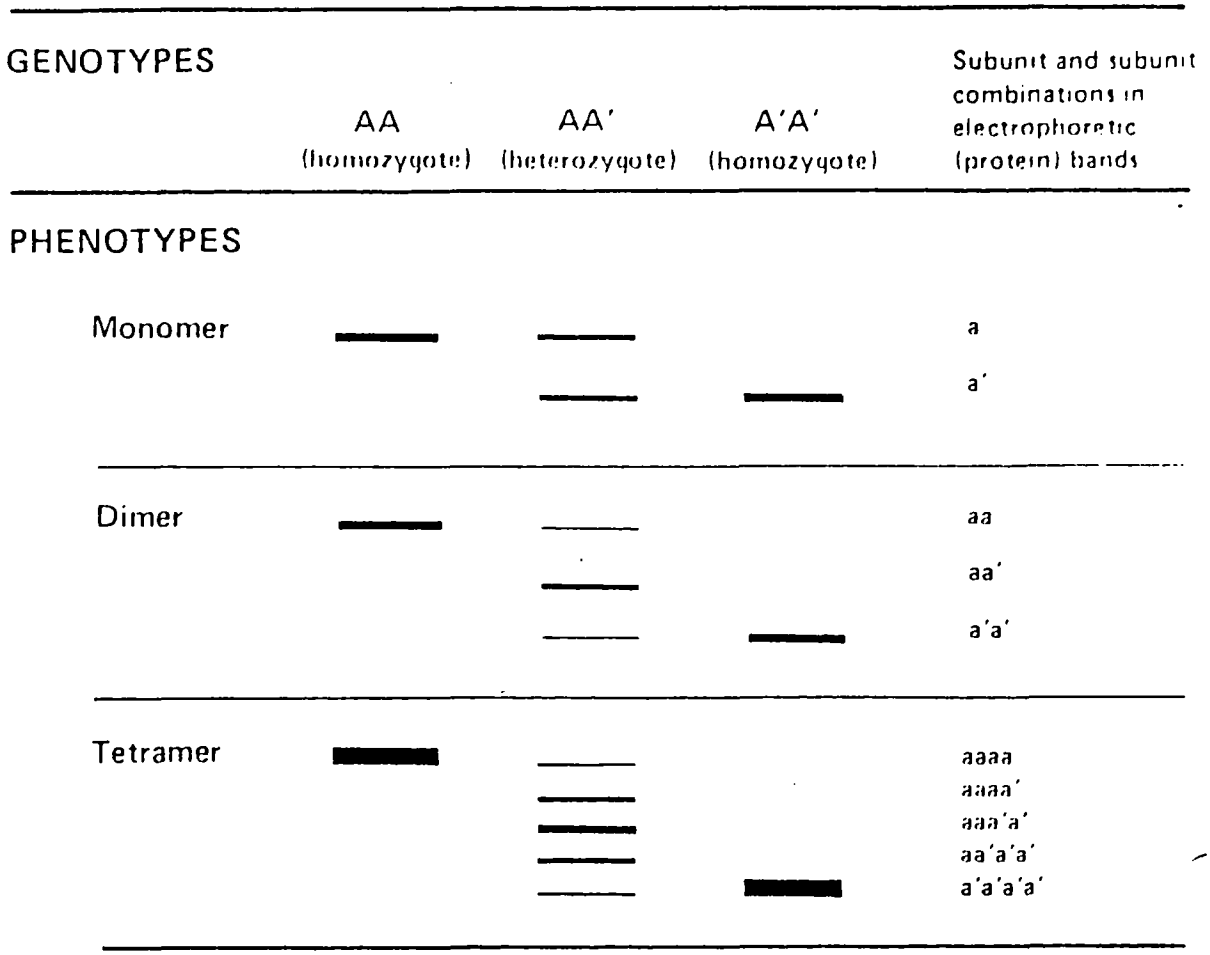


Figure 1: Electrophoretic phenotypes when one locus is expressed. Individuals are homozygous and heterozygous at loci coding for monomeric, dimeric, and tetrameric proteins: the locus is polymorphic, with alleles *A* and *A'* resulting in subunits *a* and *a'*, respectively.

(Taken from Utter *et al*., 1987).

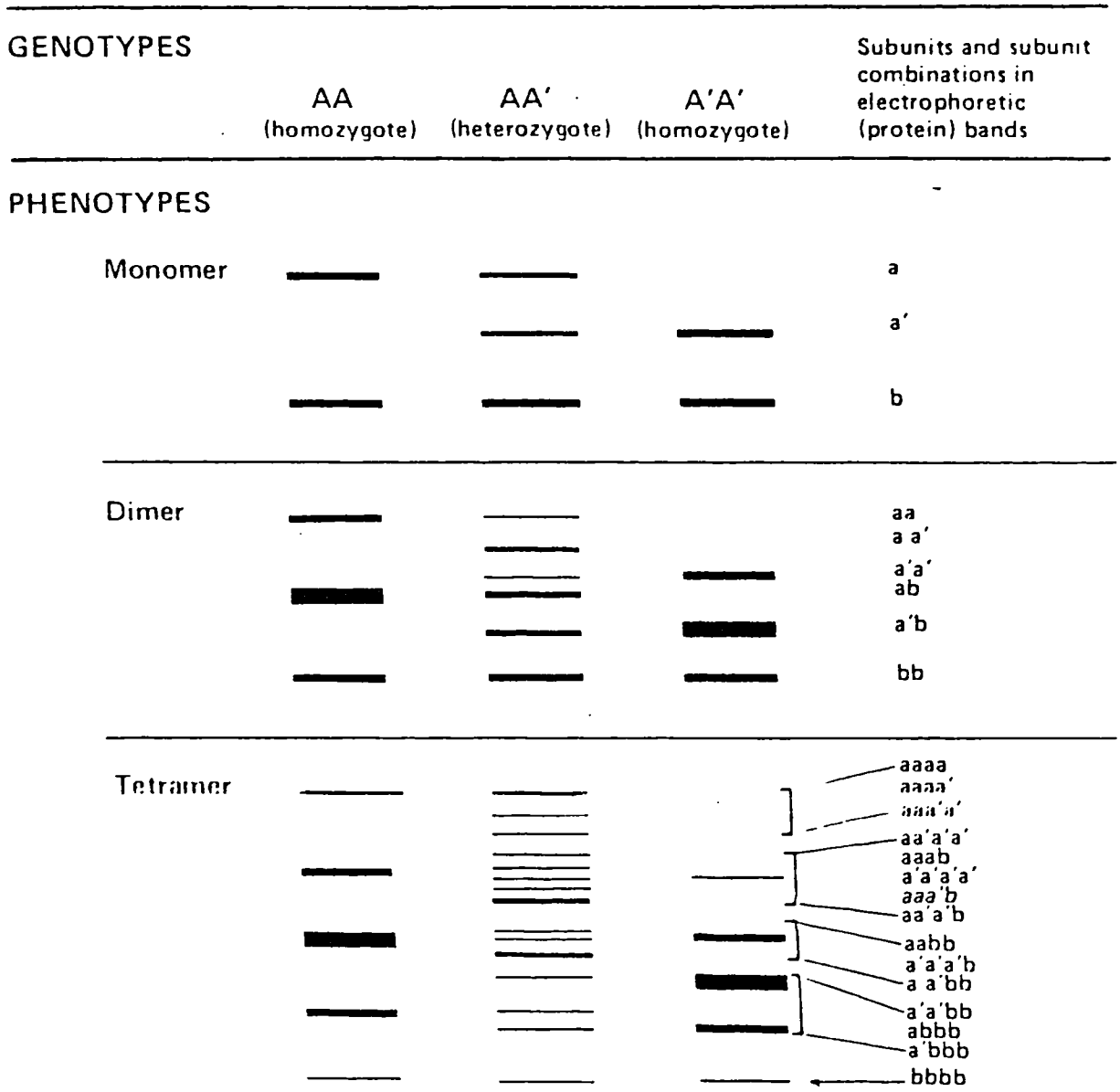


Figure 2: Electrophoretic phenotypes when two loci are expressed. Individuals are homozygous and heterozygous at loci coding for monomeric, dimeric, and tetrameric proteins: one locus is polymorphic (with alleles *A* and *A'* resulting in subunits *a* and *a'*, respectively); and a second is monomorphic, coding for a subunit (*b*) with an electrophoretic mobility that differs from subunits *a* and *a'*. Taken from (Utter *et al* ., 1987).

represent a mixture of fast- and slow-migratory sub-unit forms that occur in the corresponding homozygotes and usually at a greater intensity.

Complicated patterns arise when a protein is encoded by two or more loci (Figure 2), as they have different mobilities, or electrophoretic patterns from two or more loci whose protein bands have the same or overlapping mobilities.

The phenotypes shown in Figures 1 and 2 are known as co-dominant expressions of the respective genotypes, as all the alleles can be clearly identified. However, there are exceptions which complicate the determination of the genotype. One is the presence of isoloci (Wright *et al.* 1983), where identical sub-units are produced by two different loci. Figure 3 illustrates what may occur when the products of the second allele are identical to the first. Part of the problem is that it is almost impossible to assign alleles to specific loci when two or more loci code for identical sub-units electrophoretically. The problem is shown more clearly when one of the loci is monomorphic and the other is polymorphic (Figure 3).

Phenotypes of null alleles are also difficult or impossible to identify from electrophoresis (eg Lim and Bailey, 1977). The genotypic expression for those that have no null alleles and those heterozygous for null alleles, is usually ambiguous. Distinction is demonstrated in the different banding pattern intensities on the basis of different gene dosages. Detection of null alleles is difficult in heterozygous genotypes when only on a single locus. The only clue under such circumstances is reduced intensity of the single band. The existence of the null allele is usually verified by the absence of any electrophoretic banding pattern from homozygotes for the null allele (Utter *et al.*,1984). Hence quantitative differences in the absence of homozygous individuals for the null allele cannot be reliably identified.

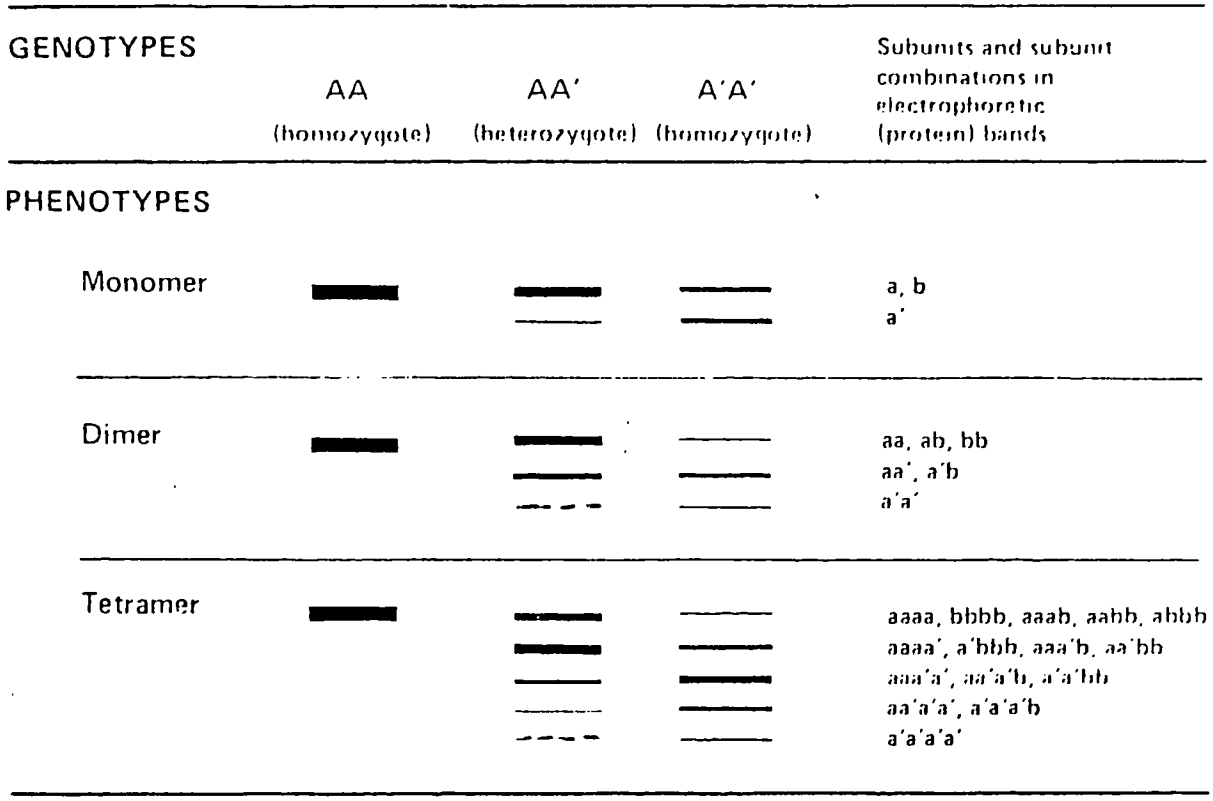


Figure 3: Electrophoretic phenotypes when isoloci are expressed. Individuals are homozygous and heterozygous at loci coding for monomeric, dimeric, and tetrameric proteins: one locus is polymorphic (with alleles *A* and *A'* resulting from subunits *a* and *a'*, respectively); and a second locus is monomorphic, coding for a subunit (*b*) with an electrophoretic mobility identical to that of subunit (*a*). (Figure taken from Utter *et al.*, 1987).

LIMITATIONS TO ELECTROPHORESIS

Although electrophoresis is widely used, it does have its limitations. The genes surveyed are structural genes coding for soluble proteins. This can be misleading in estimating genetic polymorphism. Recent studies have also suggested that in natural populations significant variation may be due to interactions between loci. This 'regulatory variation' may only alter the final gene product expression and not its structure and hence not be detected by electrophoresis (McDonald,1983).

Electrophoresis detects only a proportion of the possible variants at a locus due to undetected heterogeneity within a single band (Johnson, 1977; Coyne, 1982). This is because when samples from two different individuals exhibit bands at the same position in the gel, it cannot be concluded that they are genetically identical.

Also only a third of all amino acid substitutions are detected because of no alteration in charge. Sixteen of the more common amino acids are close to being electrically neutral in the pH range used in electrophoresis. Carrying out electrophoresis on buffers of different pH can reveal different variants (Beaumont *et al.*, 1988).

ELECTROPHORETIC STUDIES ON *POTAMOPYRGUS JENKINSI*

Electrophoretic studies on the three morphological strains A, B and C of *Potamopyrgus jenkinsi* have been carried out by Johnson (1981), Foltz *et al.* (1984) and Hauser *et al.* (1992). Johnson carried out an extensive survey on the genetics of the three strains, which confirmed Warwick's (1952) morphological division of the strains. He also compared them to the New Zealand species *Potamopyrgus antipodarum* , *P.estuarinus* and *P.nigra* in order to determine which of these three the British strains are most closely related to, as their origin had been much debated (e.g. Bodesen and Kaiser, 1949; Winterbourn, 1970;1972). Johnson's study (1981) confirmed the strains to be closely

related to *Potamopyrgus antipodarum* especially strain A. However, he also found strains B and C to be more closely related to each other than they are to strain A.

Foltz's *et al.* study (1984), too, recognised Warwick's division of the strains. But in this study a much rarer strain recognised by Warwick (personal communication to Foltz), strain D, appeared to constitute a homogeneous, electrophoretically distinct form, while strains A and C appeared to be heterogeneous assemblages of clones (Foltz *et al.*, 1984). Hauser *et al* (1992) recent multi locus DNA fingerprinting study of the three strains A, B and C, however, showed them to be monoclonal even when collected across large geographic distances.

AIMS

The aims of this study was to confirm the experimental findings shown in the previous chapters that the strains differed genetically and so to compare it to the differences observed in their life history traits when under stress and in optimal conditions. Thus the electrophoretic studies were to: 1. confirm the findings of Johnson (1981). 2. Determine from both clonal rearing (whereby the mothers and the matured daughter are electrophoresed on the same gel) and 3. periodic sampling (to discount the effect of the environment when the strains were placed in the manipulated environments), that the isozyme patterns noted were of a genetic basis.

As well as considering genetic variation between the strains, also to be examined were trade-offs at the genetic level. This is considered to be of great importance (Bell and Koufopanou, 1986) and of greater evolutionary significance (Reznick, 1985) than physiological trade-offs. Past workers have obtained conflicting results when the two types of trade-offs (eg Moller *et al.*, 1989ab; Stearns *et al.*, 1991) have been investigated on the same species.

Difference in results has been suggested to be due selection and inbreeding experiments (Reznick, 1985; Moller *et al.*, 1989ab) which are required when dealing with a sexual species. However, *Potamopyrgus jenkinsi* is an apomictic parthenogen. Thus no selection of traits is necessary and so what is observed at the phenotype should be observed at the genotype.

SAMPLING SITES

Populations of *Potamopyrgus jenkinsi* were sampled at eight locations in North Wales (Figure 4) as mentioned in chapter 1. In addition to the North Wales populations, two Scottish populations were studied: Barnes Ness (Strain A) and Barnes West (strain B), both of which were supplied by T.Warwick. No strain B populations were encountered in North Wales.

All populations were maintained in the way described in chapter 1, in separate plastic containers measuring 15cm by 30cm by 10cm. Strain B population was kept in 5% seawater as described by T.Warwick (personal communication).

Two electrophoretic methods were employed, polyacrylamide gel and cellulose acetate gels.

Polyacrylamide when set is flexible and can be handled quite easily. However the gel is brittle, and although Johnson (1981) managed to slice the gel and so stain for many more enzymes, this was not successful in this study as even when the gel was made quite thick, it tended to break when sliced.

Cellulose acetate uses the same principle as gel polyacrylamide except there is a shorter running time (30-40 minutes).

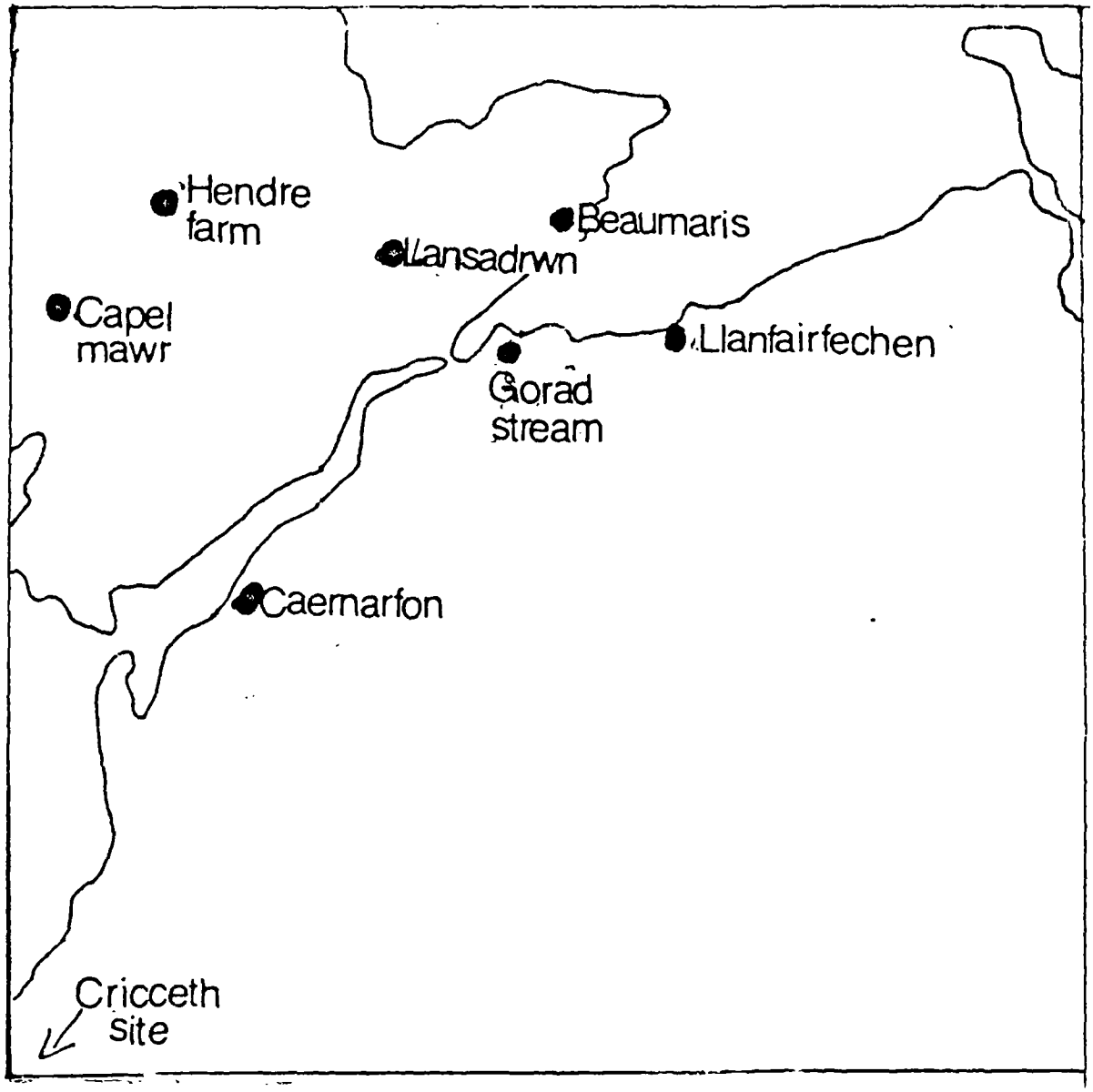


Figure 4: Sampling site areas to obtain snails for electrophoresis.

MATERIALS AND METHOD

1.POLYACRYLAMIDE GEL ELECTROPHORESIS

Extraction Method

Individual whole snails were placed in 1ml vials in a container of ice. The snails were macerated using a fine glass rod, after adding 1 spatula of acid washed sand to aid grinding and 5 drops of 40% sucrose solution which assist in halting the breakdown of enzymes. The homogenate was centrifuged for 5 minutes and allowed to settle. At all times care was taken to ensure that the vials remained cold in order to protect the enzymes from denaturing. The supernatant in the vial was then withdrawn using a drop pipette for electrophoresis. The extracts were stored in large sealed plastic containers and placed in the deep freeze at -45^{0}C. Although the extract was usually used within one week of its production, clearer results were obtained when fresh preparations were used for each electrophoretic procedure.

Preparation of Mould

The gel was prepared in a mould which (Figure 5) consisted of two Perspex plates measuring 30cm by 15cm. One plate was flat, while the other consisted of raised perspex at one end in order to create 15 pockets in the gel. A rubber gasket was moistened with distilled water and set around the edge of one of the plates. The other plate was placed on top and the two plates were held together with bulldog clips as shown in Figure 5.

Preparation of buffer solution

45.5g Tris (hydroxymethyl) aminomethane (Sigma) and 20g of glycine was dissolved in 4l of distilled water obtaining a pH of 9. The buffer solution is used in the preparation of gel and electrode buffer.

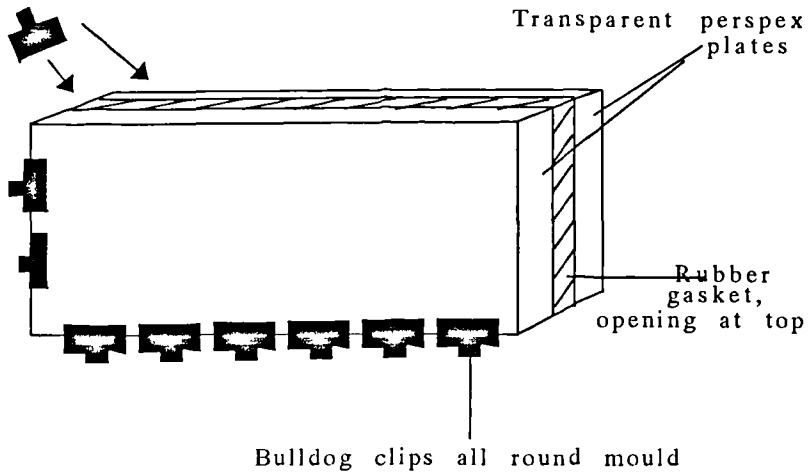


Figure 5: Preparation of gel in mould.

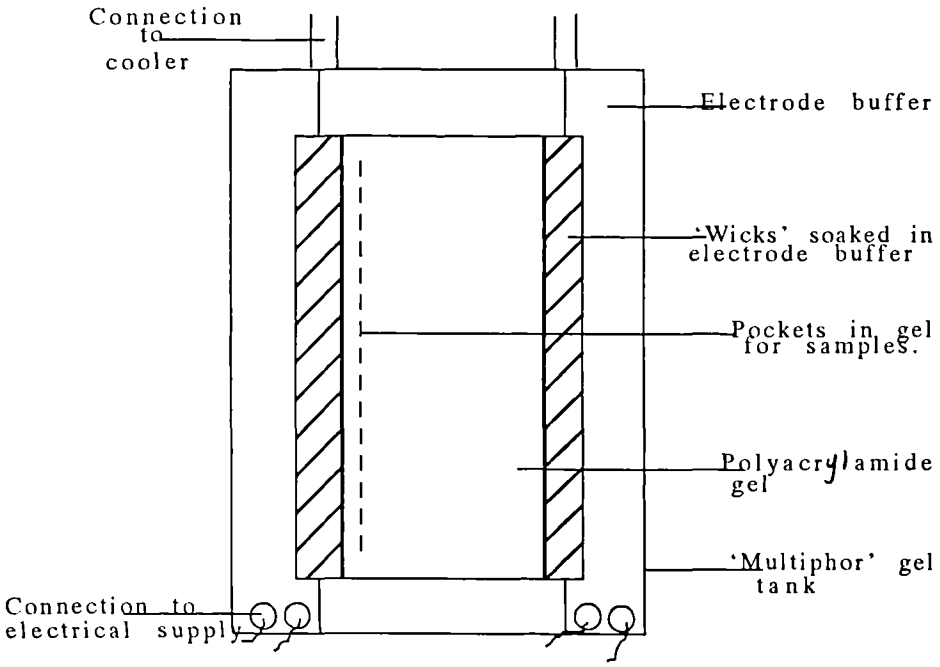


Figure 6: Set up of electrophoretic apparatus

Preparation of electrophoretic gels

7.5% polyacrylamide gel was prepared by either dissolving 4.8g of acrylamide and 0.13g bis-acrylamide in 65cm^3 of gel buffer or by dissolving 16cm^3 of protogel in 49cm^3 of gel buffer. 40µl of n, n^1, n^1-Tetramethyl-ethylene diamine (Temed)was added and finally 1cm^3 of ammonium persulphate (10%). The solution was quickly stirred and the liquid pipetted into the prepared mould through an opening in the gasket. The gel was allowed to set and taken out of the mould and placed onto the electrophoresis tank.

The electrophoresis tank (Figure 6) is connected to the a power pack and a cooler. The cooler is connected to a slab on which the gel sits. The electrode buffer is poured into pockets next to the slab. Once the gel is on the cooled slab a safety lid is placed on top and the tank is switched on.

Gel run

Before the samples were run, the gel pockets were filled with gel buffer and run for 30 minutes at 50 volts. After the run the buffer was blotted from the pockets with tissue and the supernatant samples loaded. Another run is performed for 30 minutes at 50 volts and then the voltage is raised to 250 volts and run for 4hours. For the main run a marker dye is applied to one of the pockets as a measure of the distance travelled of the enzymes in the gel.

After the main run, the gel is removed from the slab onto a glass plate and stained for the appropriate enzymes.

Table 1: List of the enzymes srceened in strain A, B and C populations. Listed are whether they were (*) screened using polyacrylamide gel, (+) screened on celllose acetate.

ENZYME	ELECTROPHORETIC SYSTEM
AAT (Aspartate amino transforase)	+
ACP (Acid phosphotase)	*
ADK (Adenosine kinase)	
AK (Adenylate kinase)	+
AMY (α-Amylase)	+
EST (α-Esterase)	*
GOT (Glutamate-oxaloacetate transaminase)	*
GPI (Glucose phosphate isomerase)	*/+
HK (Hexokinase)	+
ME (Malic Enzyme)	*
MDH (Malate dehydrogenase)	*/+
PG_6D (Phosphogluconate dehydrogenase)	*/+
PGM (Phosphoglucotomase)	*/+
SOD (Superoxide dismutase)	*
APK (Arginine phosphokinase)	+
AP (Amino peptidase)	+

2. Cellulose Acetate Method

Extraction Method

Individual snails were placed in 1ml vials and homogenised using a variable speed stirrer. The samples were immediately transferred onto the gel with the use of an applicator.

Gel run

The run was carried out for 20 minutes at 200volts using tris maleate buffer, pH9.

The isozymes were stained and placed in an oven (40^0C) for a few minutes for the bands to appear. The enzymes studied under gel and cellulose acetate electrophoresis are listed in Table 1.

RESULTS

Results that produced banding patterns from polyacrylamide gel electrophoresis are shown in figures 7-9. Those obtained from cellulose acetate are shown in plate 1-2 and figures 10-11.

Preliminary analysis showed results from frozen samples did not resolve as well as freshly prepared samples.

Before any of the aims listed above could be carried out, the enzymes needed to be screened on 20 to 30 individuals per population. However, in some populations this criteria was not met as their natural population sizes were small. Enzymes chosen would be those that gave clear repeatable results and showed differences between the strains. Unfortunately in this study the results were too ambiguous to be reliable. Either no difference was shown or if a difference was observed, it was not repeatable.Although the same staining techniques were used as that of Johnson (1981), inconclusive results were

Table 2: Results from electrophoresis study showing whether the outcome was positive (+) or negative (-) and the number of bands that appeared for each strain. The results with an * were those obtained using polyacrylamide gel and those with an x were obtained on cellulose acetate.

Enzyme	Strain A		Strain B		Strain C	
	Banding	No.	Banding	No.	Banding	No.
*MDH	+	2	+	2	+	2
*EST	+	1/2	+	2	+	2
*ACP	-		-		-	
*PGM	+	1	+	1	+	1
*GPI	+	1	+	1	+	1
*G_6PD	-		-		-	
*GOT	-		-		-	
*SOD	-		-		-	
xAP	+	3/4	+	2/3	+	3
xAAT	+	1	+	1	+	1
xMDH	+	1	+	1	+	1
xGPI	+	1	+	1	+	1
xAPK	-		+	3	+	3
xPGM	+	1	+	1	+	1
xAMY	+	2	+	2	+	1/3
xGPGDH	+	1	+	1	+	1
xHK	-		-		-	

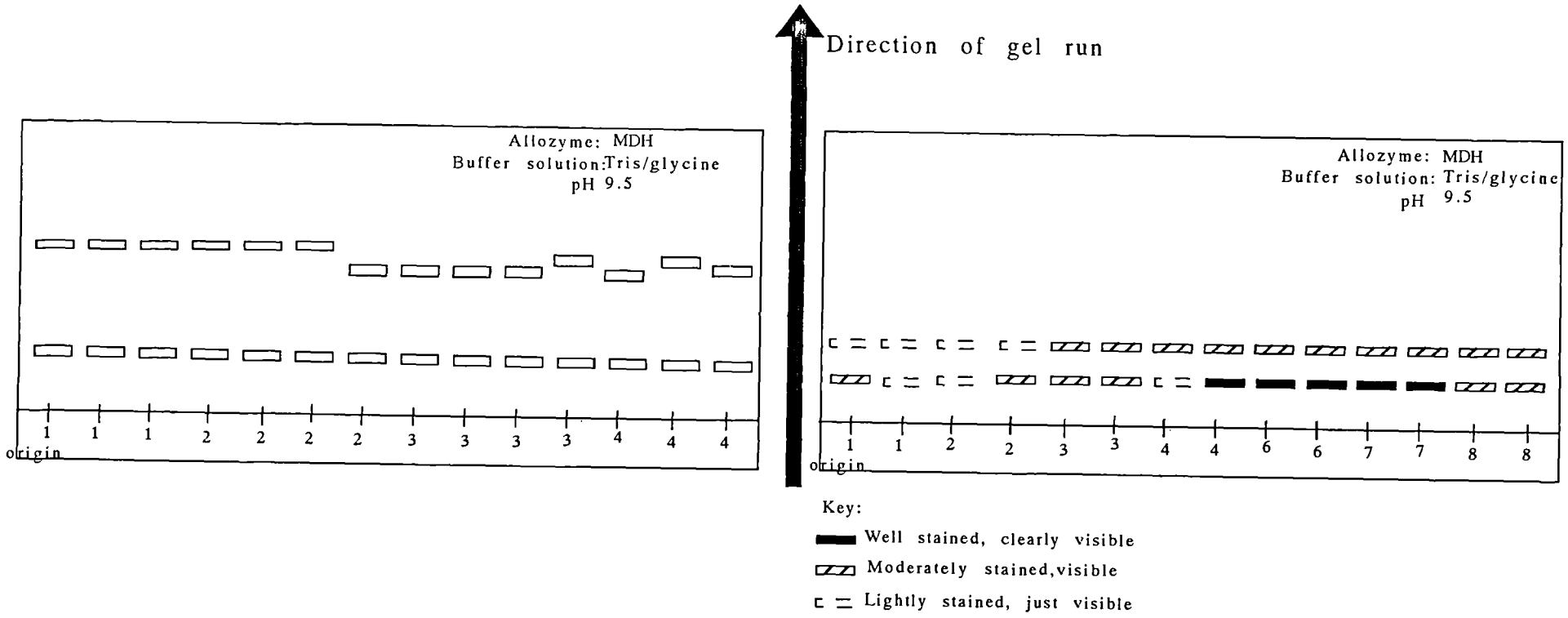


Figure 7: Zymograms of MDH (Malate dehydrogenase) for strains A,B and C at (1) Llanfairfechen, strain C; (2) Gorad stream, Bangor, strain A; (3) Llansadwrn, Anglessey, strain A; (5) Criccieth, strain A; (6) Criccieth, strain C; (7) Barnes Ness, Scotland, strain A; and (8) Barnes West, Scotland, strain B. Both gels were run at 4 C and 240V. Gels were left over night in a dark drawer. Banding patterns appeared the next day.

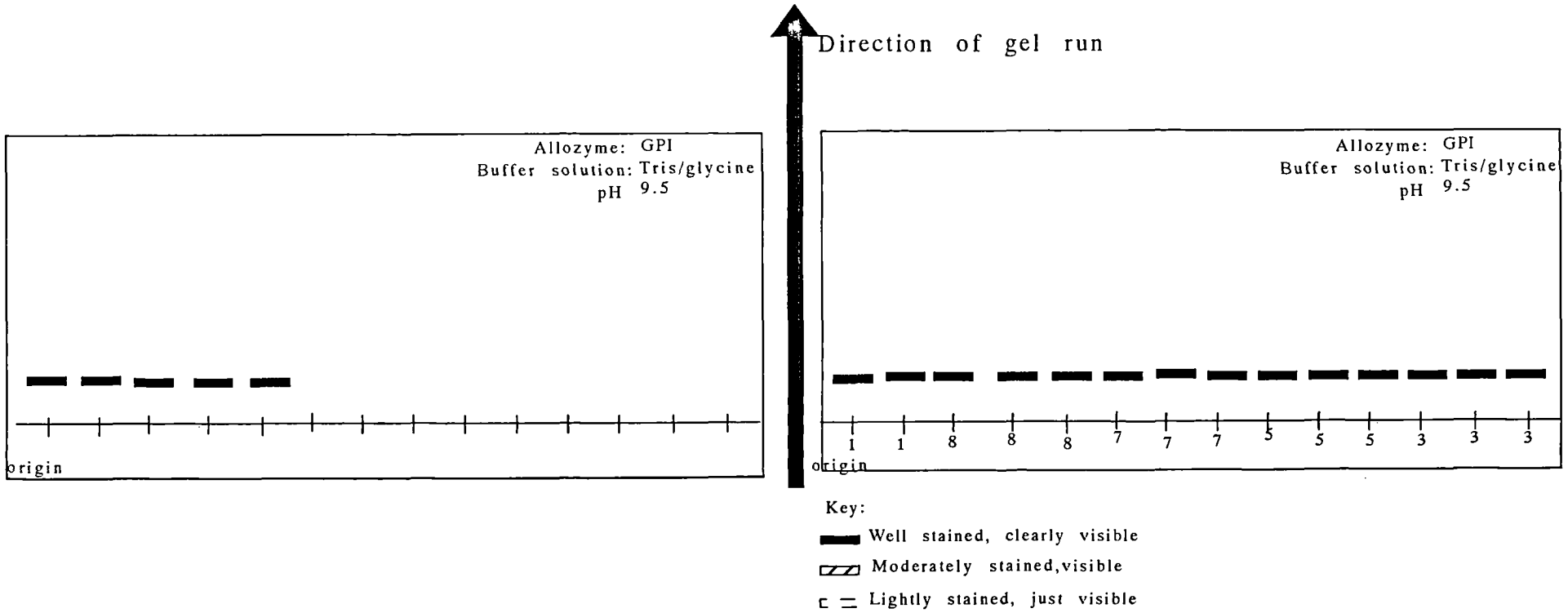


Figure 8: Zymograms of GPI (Glucose phosphoisomerase)for strains A,B and C at populations (1) Llanfairfechen, strain C; (3) Llansadwrn, strain A; (5) Criccieth, strain A; (6) Criccieth, strain C; (7) Barnes Ness, Scotland, strain A; (8) Barnes West, Scotland, strain B. Both gels were run at 4 C and at 240V. Gels were left over night for banding patterns to appear.

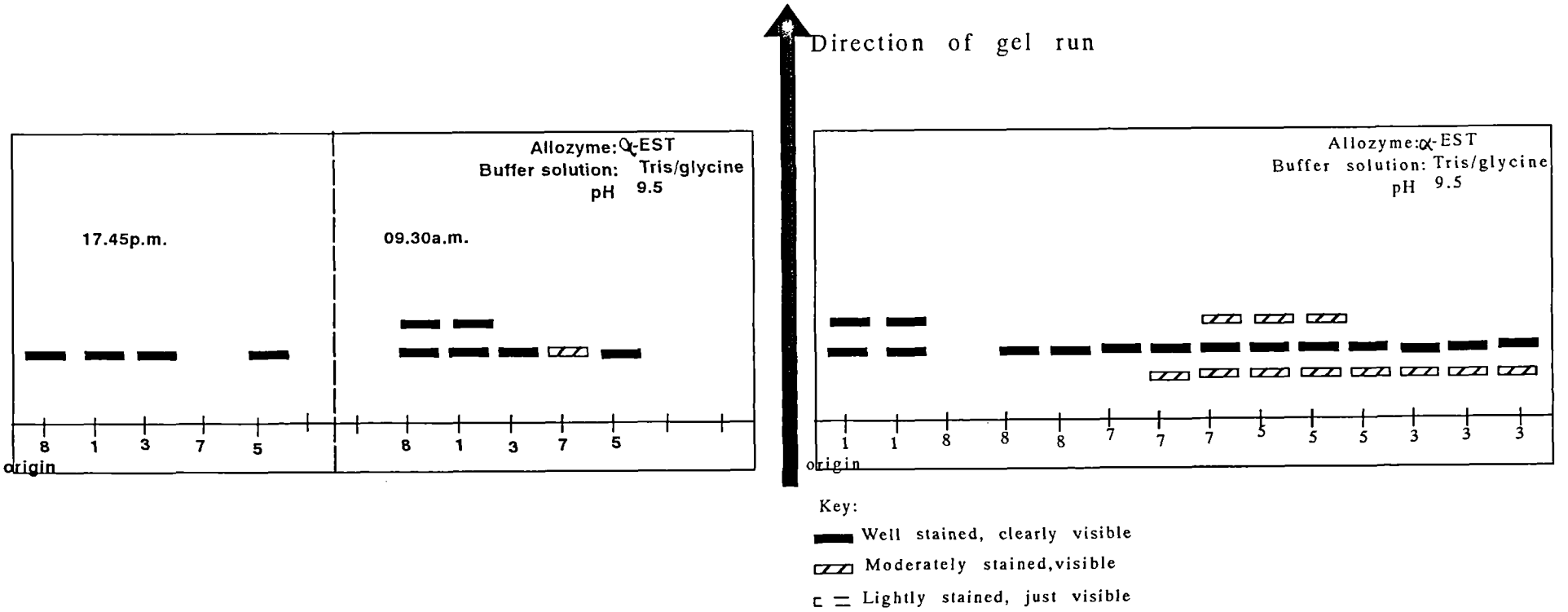


Figure 9: Zymograms of α-est (α-esterase) for strains A,B and C at populations (1) Llanfairfechan, strain C; (3) Llansadwrn, strain A; (5) Criccieth, strain A; (7) Barnes Ness, Scotland, strain A; and (8) Barnes West, Scotland, strain B. Both gels were run at 4 C and at 240V. Gels were left over night for banding banding patterns to appear.

Plate 1: Zymograms of strain A and C from (1) Llansadwrn, strain A, (2) Barnes Ness, strain A, (3) Barnes West, strain B, and (4) Llanfairfechan, strain C. The numbers by the enzyme abbreviations represent the trial number.

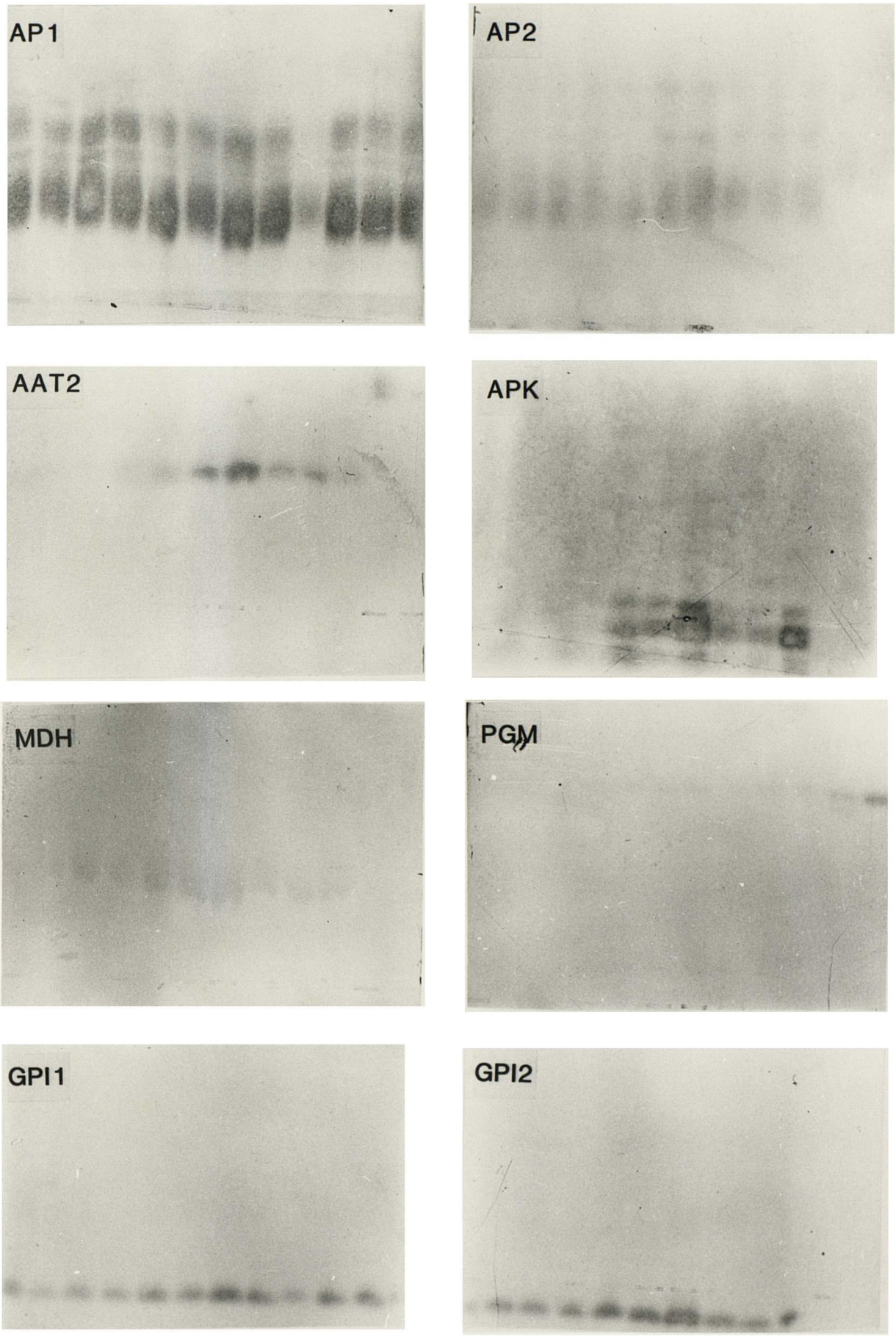

AP1
AP2
AAT2
APK
MDH
PGM
GPI1
GPI2

Figure 10: Diagramatic representation of the zymograms shown in plate 1.

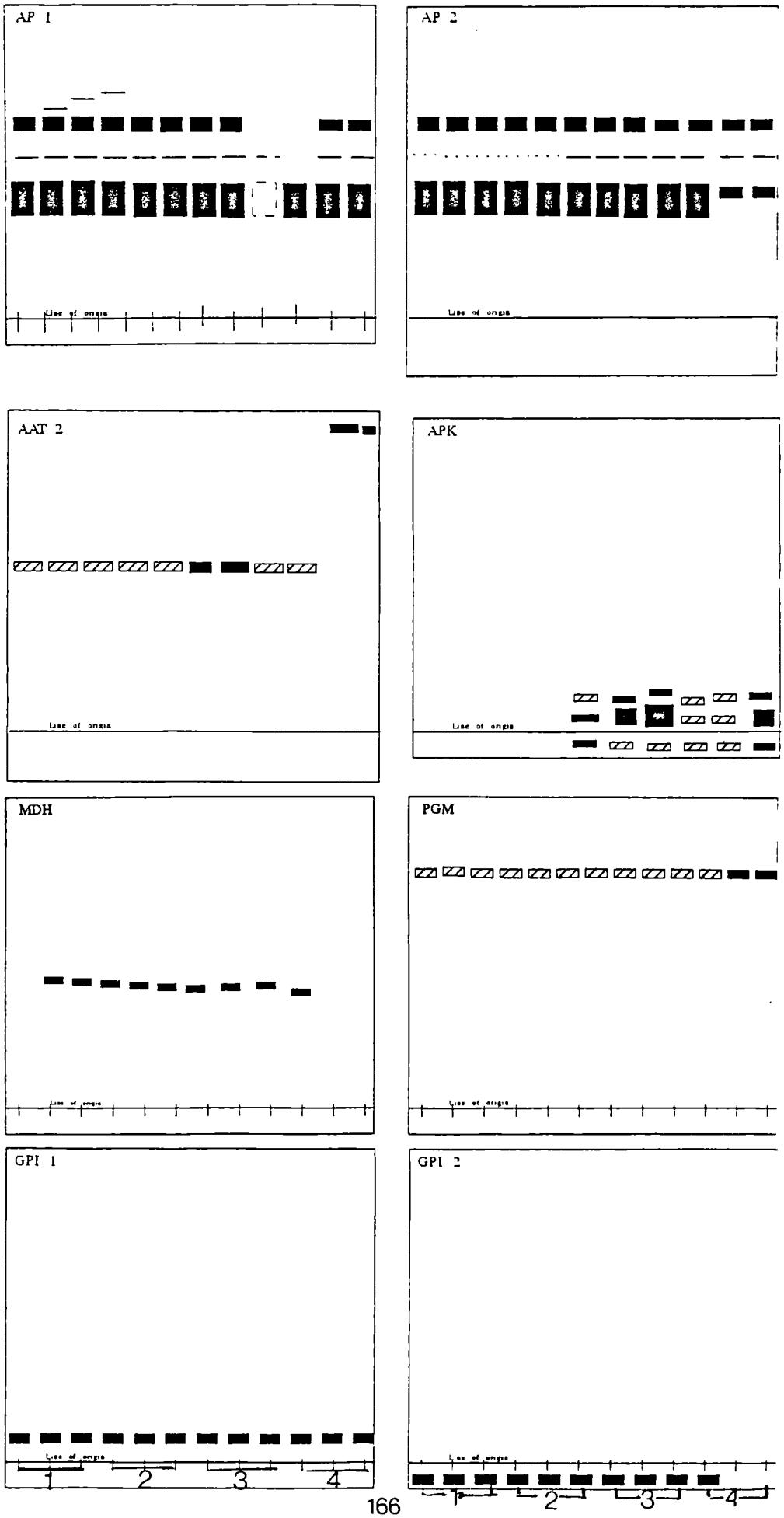
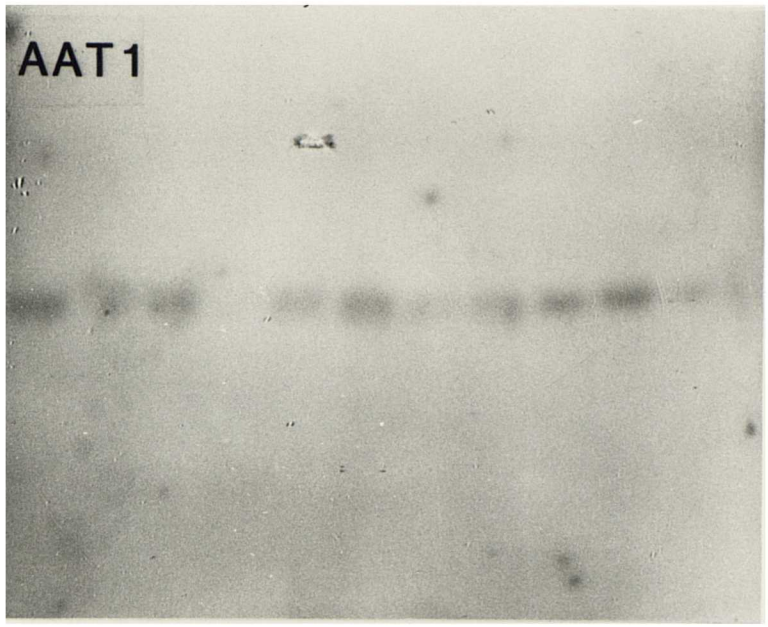
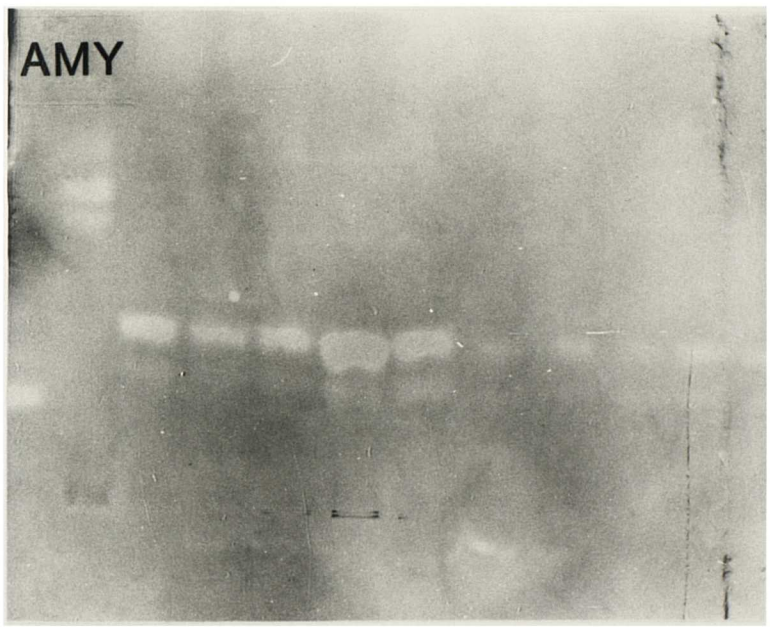
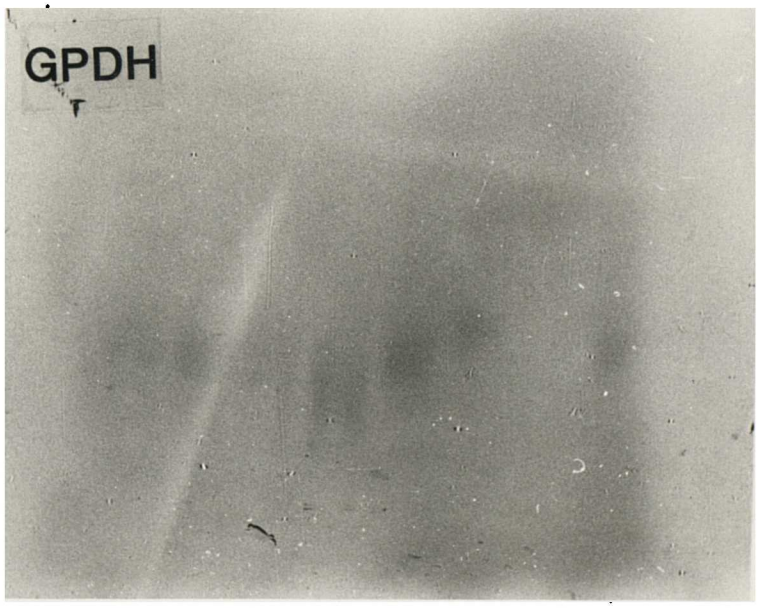


Plate 2: Zymograms of strain A and C from (1) Llanfairfechan, strain C, (2) Barnes West, strain B, (3) Barnes Ness, strain A, (4) Llansadwrn, strain A. The numbers by the enzyme abbreviations represent the trial number.


AAT1


AMY


GPDH

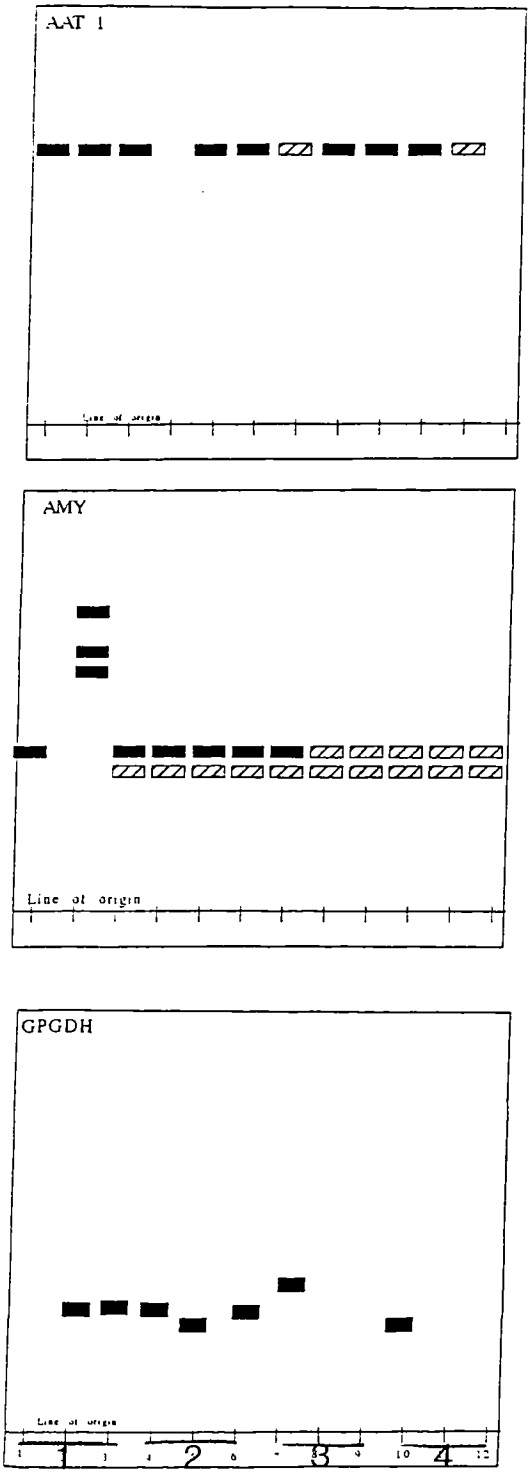


Figure 11: Diagramatic representation of plate 2.

obtained. Changes to the buffer pH usually resulted in no banding patterns.

The cellulose acetate electrophoresis gave more promising results in that banding patterns appeared in all the tested enzymes. However, the results were not repeatable.

Because the screening of enzymes was not successful, the main aim of the electrophoresis study was not achieved. However, the fact that *Potamopyrgus jenkinsi* is an apomictic clonal organism, the offspring should be identical to the parent. Thus the differences demonstrated in the two strains life-history traits (chapters 2-4) can be expected to be the same at the genotype. Indeed the results obtained from the ecophysiology of the two strains agree with the genetic studies that the strains are different (Johnson, 1981; Hauser *et al.*, 1992). The common environment experiment (chapter 2) is in itself a study of the genetic variation between the strains as any environmental influences are removed. Thus any remaining variation is due to the genetic background (Bradshaw, 1984).

APPENDIX 2:

LIFE TABLES

LIFE TABLE SURVIVAL FOR STRAIN A

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	88.0	0.0	88.0	0.0	0.0000	1.0000	1.0000
2.0	88.0	0.0	88.0	0.0	0.0000	1.0000	1.0000
4.0	88.0	0.0	88.0	20.0	0.2273	0.7727	0.7727
6.0	68.0	0.0	68.0	5.0	0.0735	0.9265	0.7159
8.0	63.0	0.0	63.0	2.0	0.0317	0.9683	0.6932
10.0	61.0	0.0	61.0	6.0	0.0984	0.9016	0.6250
12.0	55.0	0.0	55.0	0.0	0.0000	1.0000	0.6250
14.0	55.0	0.0	55.0	0.0	0.0000	1.0000	0.6250
16.0	55.0	0.0	55.0	0.0	0.0000	1.0000	0.6250
18.0	55.0	0.0	55.0	0.0	0.0000	1.0000	0.6250
20.0	55.0	0.0	55.0	2.0	0.0364	0.9636	0.6023
22.0	53.0	0.0	53.0	2.0	0.0377	0.9623	0.5795
24.0	51.0	0.0	51.0	1.0	0.0196	0.9804	0.5682
26.0	50.0	0.0	50.0	0.0	0.0000	1.0000	0.5682
28.0	50.0	0.0	50.0	1.0	0.0200	0.9800	0.5568
30.0	49.0	0.0	49.0	4.0	0.0816	0.9184	0.5114
32.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
34.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
36.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
38.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
40.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
42.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
44.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
46.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
48.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.5114
50.0	45.0	0.0	45.0	6.0	0.1333	0.8667	0.4432
52.0	39.0	0.0	39.0	2.0	0.0513	0.9487	0.4205
54.0	37.0	37.0	18.5	0.0	0.0000	1.0000	0.4205

MEDIAN SURVIVAL TIME FOR THESE DATA IS

LIFE TABLE SURVIVAL FOR STRAIN C

VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	88.0	0.0	88.0	0.0	0.0000	1.0000	1.0000
2.0	88.0	0.0	88.0	14.0	0.1591	0.8409	0.8409
4.0	74.0	0.0	74.0	6.0	0.0811	0.9189	0.7727
6.0	68.0	0.0	68.0	2.0	0.0294	0.9706	0.7500
8.0	66.0	0.0	66.0	0.0	0.0000	1.0000	0.7500
10.0	66.0	0.0	66.0	2.0	0.0303	0.9697	0.7273
12.0	64.0	0.0	64.0	0.0	0.0000	1.0000	0.7273
14.0	64.0	0.0	64.0	0.0	0.0000	1.0000	0.7273
16.0	64.0	0.0	64.0	0.0	0.0000	1.0000	0.7273
18.0	64.0	0.0	64.0	0.0	0.0000	1.0000	0.7273
20.0	64.0	0.0	64.0	0.0	0.0000	1.0000	0.7273
22.0	64.0	0.0	64.0	1.0	0.0156	0.9844	0.7159
24.0	63.0	0.0	63.0	0.0	0.0000	1.0000	0.7159
26.0	63.0	0.0	63.0	0.0	0.0000	1.0000	0.7159
28.0	63.0	0.0	63.0	1.0	0.0159	0.9841	0.7045
30.0	62.0	0.0	62.0	2.0	0.0323	0.9677	0.6818
32.0	60.0	0.0	60.0	0.0	0.0000	1.0000	0.6818
34.0	60.0	0.0	60.0	0.0	0.0000	1.0000	0.6818
36.0	60.0	0.0	60.0	0.0	0.0000	1.0000	0.6818
38.0	60.0	0.0	60.0	1.0	0.0167	0.9833	0.6705
40.0	59.0	0.0	59.0	0.0	0.0000	1.0000	0.6705
42.0	59.0	0.0	59.0	0.0	0.0000	1.0000	0.6705
44.0	59.0	0.0	59.0	2.0	0.0339	0.9661	0.6477
46.0	57.0	0.0	57.0	0.0	0.0000	1.0000	0.6477
48.0	57.0	0.0	57.0	0.0	0.0000	1.0000	0.6477
50.0	57.0	0.0	57.0	4.0	0.0702	0.9298	0.6023
52.0	53.0	0.0	53.0	0.0	0.0000	1.0000	0.6023
54.0	53.0	53.0	26.5	0.0	0.0000	1.0000	0.6023

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 54.00+

Section 2.3: Chapter 3

2.31

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	14.0	0.3500	0.6500	0.6500	0.075
2.0	26.0	0.0	26.0	3.0	0.1154	0.8846	0.5750	0.078
3.0	23.0	0.0	23.0	6.0	0.2609	0.7391	0.4250	0.078
4.0	17.0	0.0	17.0	0.0	0.0000	1.0000	0.4250	0.078
5.0	17.0	0.0	17.0	1.0	0.0588	0.9412	0.4000	0.077
6.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
7.0	16.0	0.0	16.0	1.0	0.0625	0.9375	0.3750	0.077
8.0	15.0	0.0	15.0	0.0	0.0000	1.0000	0.3750	0.077
9.0	15.0	0.0	15.0	1.0	0.0667	0.9333	0.3500	0.075
10.0	14.0	0.0	14.0	0.0	0.0000	1.0000	0.3500	0.075
11.0	14.0	0.0	14.0	0.0	0.0000	1.0000	0.3500	0.075
12.0	14.0	0.0	14.0	2.0	0.1429	0.8571	0.3000	0.072
13.0	12.0	0.0	12.0	1.0	0.0833	0.9167	0.2750	0.071
14.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2750	0.071
15.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2750	0.071
16.0	11.0	0.0	11.0	1.0	0.0909	0.9091	0.2500	0.068
17.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	0.068
18.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.2250	0.066
19.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.2250	0.066
20.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.2250	0.066
21.0	9.0	9.0	4.5	0.0	0.0000	1.0000	0.2250	0.066

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 3.50

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	9.0	0.2250	0.7750	0.7750	0.066
2.0	31.0	0.0	31.0	3.0	0.0968	0.9032	0.7000	0.072
3.0	28.0	0.0	28.0	5.0	0.1786	0.8214	0.5750	0.078
4.0	23.0	0.0	23.0	5.0	0.2174	0.7826	0.4500	0.079
5.0	18.0	0.0	18.0	0.0	0.0000	1.0000	0.4500	0.079
6.0	18.0	0.0	18.0	2.0	0.1111	0.8889	0.4000	0.077
7.0	16.0	0.0	16.0	4.0	0.2500	0.7500	0.3000	0.072
8.0	12.0	0.0	12.0	0.0	0.0000	1.0000	0.3000	0.072
9.0	12.0	0.0	12.0	2.0	0.1667	0.8333	0.2500	0.068
10.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	0.068
11.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.2250	0.066
12.0	9.0	0.0	9.0	1.0	0.1111	0.8889	0.2000	0.063
13.0	8.0	0.0	8.0	2.0	0.2500	0.7500	0.1500	0.056
14.0	6.0	0.0	6.0	2.0	0.3333	0.6667	0.1000	0.047
15.0	4.0	0.0	4.0	2.0	0.5000	0.5000	0.0500	0.034
16.0	2.0	0.0	2.0	1.0	0.5000	0.5000	0.0250	0.025
17.0	1.0	0.0	1.0	1.0	1.0000	0.0000	0.0000	0.000

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 4.60

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	3.0	0.0750	0.9250	0.9250	0.042
3.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.042
4.0	37.0	0.0	37.0	4.0	0.1081	0.8919	0.8250	0.060
5.0	33.0	0.0	33.0	1.0	0.0303	0.9697	0.8000	0.063
6.0	32.0	0.0	32.0	5.0	0.1563	0.8438	0.6750	0.074
7.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
8.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
9.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
10.0	27.0	0.0	27.0	1.0	0.0370	0.9630	0.6500	0.075
11.0	26.0	0.0	26.0	3.0	0.1154	0.8846	0.5750	0.078
12.0	23.0	0.0	23.0	1.0	0.0435	0.9565	0.5500	0.079
13.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.079
14.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.079
15.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.079
16.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.079
17.0	22.0	0.0	22.0	1.0	0.0455	0.9545	0.5250	0.079
18.0	21.0	0.0	21.0	0.0	0.0000	1.0000	0.5250	0.079
19.0	21.0	0.0	21.0	1.0	0.0476	0.9524	0.5000	0.079
20.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.079
21.0	20.0	20.0	10.0	0.0	0.0000	1.0000	0.5000	0.079

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 21.00+

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9750	0.025
2.0	39.0	0.0	39.0	3.0	0.0769	0.9231	0.9000	0.047
3.0	36.0	0.0	36.0	13.0	0.3611	0.6389	0.5750	0.078
4.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.5750	0.078
5.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.5750	0.078
6.0	23.0	0.0	23.0	8.0	0.3478	0.6522	0.3750	0.077
7.0	15.0	0.0	15.0	6.0	0.4000	0.6000	0.2250	0.066
8.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.2250	0.066
9.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.2250	0.066
10.0	9.0	0.0	9.0	3.0	0.3333	0.6667	0.1500	0.056
11.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1500	0.056
12.0	6.0	0.0	6.0	1.0	0.1667	0.8333	0.1250	0.052
13.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
14.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
15.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
16.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
17.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
18.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
19.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
20.0	5.0	0.0	5.0	0.0	0.0000	1.0000	0.1250	0.052
21.0	5.0	5.0	2.5	0.0	0.0000	1.0000	0.1250	0.052

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 6.38

2.32

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	4.0	0.1000	0.9000	0.9000	0.047
2.0	36.0	0.0	36.0	2.0	0.0556	0.9444	0.8500	0.056
3.0	34.0	0.0	34.0	1.0	0.0294	0.9706	0.8250	0.060
4.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250	0.060
5.0	33.0	0.0	33.0	3.0	0.0909	0.9091	0.7500	0.068
6.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.7500	0.068
7.0	30.0	0.0	30.0	1.0	0.0333	0.9667	0.7250	0.071
8.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
9.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
10.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
11.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
12.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.7000	0.072
13.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
14.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
15.0	28.0	0.0	28.0	1.0	0.0357	0.9643	0.6750	0.074
16.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
17.0	27.0	0.0	27.0	1.0	0.0370	0.9630	0.6500	0.075
18.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.075
19.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.075
20.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.075
21.0	26.0	26.0	13.0	0.0	0.0000	1.0000	0.6500	0.075

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 21.00+

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
2.0	38.0	0.0	38.0	2.0	0.0526	0.9474	0.9000	0.047
3.0	36.0	0.0	36.0	1.0	0.0278	0.9722	0.8750	0.052
4.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
5.0	35.0	0.0	35.0	2.0	0.0571	0.9429	0.8250	0.060
6.0	33.0	0.0	33.0	1.0	0.0303	0.9697	0.8000	0.063
7.0	32.0	0.0	32.0	1.0	0.0313	0.9688	0.7750	0.066
8.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.7750	0.066
9.0	31.0	0.0	31.0	2.0	0.0645	0.9355	0.7250	0.071
10.0	29.0	0.0	29.0	2.0	0.0690	0.9310	0.6750	0.074
11.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
12.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074

LIFE TABLE (CONTD)

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
13.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
14.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
15.0	27.0	0.0	27.0	2.0	0.0741	0.9259	0.6250	0.077
16.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.6250	0.077
17.0	25.0	0.0	25.0	2.0	0.0800	0.9200	0.5750	0.078
18.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.5750	0.078
19.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.5750	0.078
20.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.5750	0.078
21.0	23.0	23.0	11.5	0.0	0.0000	1.0000	0.5750	0.078

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 21.00+

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
2.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
3.0	38.0	0.0	38.0	6.0	0.1579	0.8421	0.8000	0.063
4.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
5.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
6.0	32.0	0.0	32.0	2.0	0.0625	0.9375	0.7500	0.068
7.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.7500	0.068
8.0	30.0	0.0	30.0	2.0	0.0667	0.9333	0.7000	0.072
9.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
10.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
11.0	28.0	0.0	28.0	2.0	0.0714	0.9286	0.6500	0.075
12.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.075
13.0	26.0	0.0	26.0	2.0	0.0769	0.9231	0.6000	0.077
14.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.6000	0.077
15.0	24.0	0.0	24.0	2.0	0.0833	0.9167	0.5500	0.079
16.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.079
17.0	22.0	0.0	22.0	2.0	0.0909	0.9091	0.5000	0.079
18.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.079
19.0	20.0	0.0	20.0	2.0	0.1000	0.9000	0.4500	0.079
20.0	18.0	0.0	18.0	0.0	0.0000	1.0000	0.4500	0.079
21.0	18.0	18.0	9.0	0.0	0.0000	1.0000	0.4500	0.079

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 18.00

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
2.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
3.0	38.0	0.0	38.0	11.0	0.2895	0.7105	0.6750	0.074
4.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
5.0	27.0	0.0	27.0	1.0	0.0370	0.9630	0.6500	0.075
6.0	26.0	0.0	26.0	4.0	0.1538	0.8462	0.5500	0.079
7.0	22.0	0.0	22.0	2.0	0.0909	0.9091	0.5000	0.079
8.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.079
9.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.079
10.0	20.0	0.0	20.0	1.0	0.0500	0.9500	0.4750	0.079
11.0	19.0	0.0	19.0	2.0	0.1053	0.8947	0.4250	0.078
12.0	17.0	0.0	17.0	0.0	0.0000	1.0000	0.4250	0.078
13.0	17.0	0.0	17.0	1.0	0.0588	0.9412	0.4000	0.077
14.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
15.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
16.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
17.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
18.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
19.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
20.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
21.0	16.0	16.0	8.0	0.0	0.0000	1.0000	0.4000	0.077

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 10.00

2.23: LIFE TABLE FOR STRAIN A,ADULTS, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	3.0	0.0750	0.9250	0.9250	0.042
2.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.042
3.0	37.0	0.0	37.0	3.0	0.0811	0.9189	0.8500	0.056
4.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.8500	0.056
5.0	34.0	0.0	34.0	2.0	0.0588	0.9412	0.8000	0.063
6.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
7.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
8.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
9.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
10.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
11.0	32.0	0.0	32.0	2.0	0.0625	0.9375	0.7500	0.068
12.0	30.0	0.0	30.0	2.0	0.0667	0.9333	0.7000	0.072
13.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
14.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
15.0	28.0	0.0	28.0	2.0	0.0714	0.9286	0.6500	0.075
16.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.075
17.0	26.0	0.0	26.0	7.0	0.2692	0.7308	0.4750	0.079
18.0	19.0	0.0	19.0	2.0	0.1053	0.8947	0.4250	0.078
19.0	17.0	0.0	17.0	0.0	0.0000	1.0000	0.4250	0.078
20.0	17.0	0.0	17.0	0.0	0.0000	1.0000	0.4250	0.078
21.0	17.0	17.0	8.5	0.0	0.0000	1.0000	0.4250	0.078

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 17.86

LIFE TABLE FOR STRAIN A, ADULTS STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRING THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9750	0.025
3.0	39.0	0.0	39.0	2.0	0.0513	0.9487	0.9250	0.042
4.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.042
5.0	37.0	0.0	37.0	4.0	0.1081	0.8919	0.8250	0.060
6.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250	0.060
7.0	33.0	0.0	33.0	2.0	0.0606	0.9394	0.7750	0.066
8.0	31.0	0.0	31.0	4.0	0.1290	0.8710	0.6750	0.074
9.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
10.0	27.0	0.0	27.0	1.0	0.0370	0.9630	0.6500	0.075
11.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.075
12.0	26.0	0.0	26.0	2.0	0.0769	0.9231	0.6000	0.077
13.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.6000	0.077
14.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.6000	0.077
15.0	24.0	0.0	24.0	8.0	0.3333	0.6667	0.4000	0.077
16.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.4000	0.077
17.0	16.0	0.0	16.0	6.0	0.3750	0.6250	0.2500	0.068
18.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	0.068
19.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.2250	0.066
20.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.2250	0.066
21.0	9.0	9.0	4.5	0.0	0.0000	1.0000	0.2250	0.066

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 15.50

LIFE TABLE FOR STRAIN C, ADULTS, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
3.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
4.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
5.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
6.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
7.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
8.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
9.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
10.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
11.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
12.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
13.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
14.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
15.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
16.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
17.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
18.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
19.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
20.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
21.0	38.0	38.0	19.0	0.0	0.0000	1.0000	0.9500	0.034

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 21.00

LIFE TABLE FOR STRAIN C, ADULTS, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.00
1.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.00
2.0	40.0	0.0	40.0	3.0	0.0750	0.9250	0.9250	0.04
3.0	37.0	0.0	37.0	2.0	0.0541	0.9459	0.8750	0.05
4.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.05
5.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.8500	0.05
6.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.8500	0.05
7.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.8500	0.05
8.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.8500	0.05
9.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.8500	0.05
10.0	34.0	0.0	34.0	2.0	0.0588	0.9412	0.8000	0.06
11.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
12.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
13.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
14.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
15.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
16.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
17.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.06
18.0	32.0	0.0	32.0	2.0	0.0625	0.9375	0.7500	0.06
19.0	30.0	0.0	30.0	2.0	0.0667	0.9333	0.7000	0.07
20.0	28.0	0.0	28.0	4.0	0.1429	0.8571	0.6000	0.07
21.0	24.0	21.0	13.5	3.0	0.2222	0.7778	0.4667	0.09

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 21.75

FOOD RATION EXPERIMENT

2.24:

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.00
2.0	40.0	0.0	40.0	4.0	0.1000	0.9000	0.9000	0.47
4.0	36.0	0.0	36.0	7.0	0.1944	0.8056	0.7250	0.71
6.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.71
8.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.7000	0.72
10.0	28.0	0.0	28.0	3.0	0.1071	0.8929	0.6250	0.77
12.0	25.0	0.0	25.0	3.0	0.1200	0.8800	0.5500	0.79
14.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.79
16.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	0.79
18.0	22.0	0.0	22.0	2.0	0.0909	0.9091	0.5000	0.79
20.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.79
22.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.79
24.0+	20.0	19.0	10.5	1.0	0.0952	0.9048	0.4524	0.0 5

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, ON MEDIUM RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S OF C MUL S RV- I ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0 000
2.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0 034
4.0	38.0	0.0	38.0	3.0	0.0789	0.9211	0.8750	0 052
6.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0 052
8.0	35.0	0.0	35.0	7.0	0.2000	0.8000	0.7000	0 072
10.0	28.0	0.0	28.0	3.0	0.1071	0.8929	0.6250	0 07
12.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.6250	0 07
14.0	25.0	0.0	25.0	3.0	0.1200	0.8800	0.5500	0 07
16.0	22.0	0.0	22.0	1.0	0.0455	0.9545	0.5250	0 07
18.0	21.0	0.0	21.0	2.0	0.0952	0.9048	0.4750	0 07
20.0	19.0	0.0	19.0	5.0	0.2632	0.7368	0.3500	0 07
22.0	14.0	0.0	14.0	4.0	0.2857	0.7143	0.2500	0 06
24.0+	10.0	10.0	5.0	0.0	0.0000	1.0000	0.2500	0 06

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 19.00

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, ON LOW RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S C S I	OF MUL RV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	C	000
2.0	40.0	0.0	40.0	12.0	0.3000	0.7000	0.7000	C	07
4.0	28.0	0.0	28.0	1.0	0.0357	0.9643	0.6750	C	07
6.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	C	07
8.0	27.0	0.0	27.0	11.0	0.4074	0.5926	0.4000	C	07
10.0	16.0	0.0	16.0	4.0	0.2500	0.7500	0.3000	C	07
12.0	12.0	0.0	12.0	0.0	0.0000	1.0000	0.3000	C	07
14.0	12.0	0.0	12.0	1.0	0.0833	0.9167	0.2750	C	07
16.0	11.0	0.0	11.0	1.0	0.0909	0.9091	0.2500	C	06
18.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	C	06
20.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	C	06
22.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.2250	C	06
24.0+	9.0	8.0	5.0	1.0	0.2000	0.8000	0.1800	C	06

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 9.27

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S C S I	OF MUL RV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	C	000
2.0	40.0	0.0	40.0	6.0	0.1500	0.8500	0.8500	C	05
4.0	34.0	0.0	34.0	1.0	0.0294	0.9706	0.8250	C	06
6.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250	C	06
8.0	33.0	0.0	33.0	12.0	0.3636	0.6364	0.5250	C	07
10.0	21.0	0.0	21.0	1.0	0.0476	0.9524	0.5000	C	07
12.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	C	07
14.0	20.0	0.0	20.0	4.0	0.2000	0.8000	0.4000	C	07
16.0	16.0	0.0	16.0	12.0	0.7500	0.2500	0.1000	C	04
18.0	4.0	0.0	4.0	1.0	0.2500	0.7500	0.0750	C	04
20.0	3.0	0.0	3.0	1.0	0.3333	0.6667	0.0500	C	03
22.0	2.0	0.0	2.0	1.0	0.5000	0.5000	0.0250	C	02
24.0+	1.0	0.0	1.0	1.0	1.0000	0.0000	0.0000	C	000

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 12.00

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S C S I	OF MUL RV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	C	000
2.0	40.0	0.0	40.0	9.0	0.2250	0.7750	0.7750	C	06
4.0	31.0	0.0	31.0	3.0	0.0968	0.9032	0.7000	C	07
6.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	C	07
8.0	28.0	0.0	28.0	4.0	0.1429	0.8571	0.6000	C	07
10.0	24.0	0.0	24.0	2.0	0.0833	0.9167	0.5500	C	07
12.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.5500	C	07
14.0	22.0	0.0	22.0	5.0	0.2273	0.7727	0.4250	C	07
16.0	17.0	0.0	17.0	1.0	0.0588	0.9412	0.4000	C	07
18.0	16.0	0.0	16.0	1.0	0.0625	0.9375	0.3750	C	07
20.0	15.0	0.0	15.0	1.0	0.0667	0.9333	0.3500	C	07
22.0	14.0	0.0	14.0	0.0	0.0000	1.0000	0.3500	C	07
24.0+	14.0	14.0	7.0	0.0	0.0000	1.0000	0.3500	C	07

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 14.80

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, ON MEDIUM RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S C S I	OF MUL RV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	C	000
2.0	40.0	0.0	40.0	6.0	0.1500	0.8500	0.8500	C	05
4.0	34.0	0.0	34.0	8.0	0.2353	0.7647	0.6500	C	07
6.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	C	07
8.0	26.0	0.0	26.0	10.0	0.3846	0.6154	0.4000	C	07
10.0	16.0	0.0	16.0	2.0	0.1250	0.8750	0.3500	C	07
12.0	14.0	0.0	14.0	0.0	0.0000	1.0000	0.3500	C	07
14.0	14.0	0.0	14.0	1.0	0.0714	0.9286	0.3250	C	07
16.0	13.0	0.0	13.0	2.0	0.1538	0.8462	0.2750	C	07
18.0	11.0	0.0	11.0	1.0	0.0909	0.9091	0.2500	C	06
20.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	C	06
22.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2500	C	06
24.0+	10.0	10.0	5.0	0.0	0.0000	1.0000	0.2500	C	06

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 9.20

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, ON LOW RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S OF MUL RV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	8.0	0.2000	0.8000	0.8000	0.063
4.0	32.0	0.0	32.0	5.0	0.1563	0.8438	0.6750	0.074
6.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.6750	0.074
8.0	27.0	0.0	27.0	7.0	0.2593	0.7407	0.5000	0.079
10.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.079
12.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.5000	0.079
14.0	20.0	0.0	20.0	4.0	0.2000	0.8000	0.4000	0.077
16.0	16.0	0.0	16.0	2.0	0.1250	0.8750	0.3500	0.075
18.0	14.0	0.0	14.0	1.0	0.0714	0.9286	0.3250	0.074
20.0	13.0	0.0	13.0	4.0	0.3077	0.6923	0.2250	0.066
22.0	9.0	0.0	9.0	2.0	0.2222	0.7778	0.1750	0.060
24.0+	7.0	7.0	3.5	0.0	0.0000	1.0000	0.1750	0.060

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 14.00

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	S OF MUL RV-ING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	9.0	0.2250	0.7750	0.7750	0.066
4.0	31.0	0.0	31.0	3.0	0.0968	0.9032	0.7000	0.072
6.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
8.0	28.0	0.0	28.0	6.0	0.2143	0.7857	0.5500	0.079
10.0	22.0	0.0	22.0	8.0	0.3636	0.6364	0.3500	0.075
12.0	14.0	0.0	14.0	0.0	0.0000	1.0000	0.3500	0.075
14.0	14.0	0.0	14.0	6.0	0.4286	0.5714	0.2000	0.063
16.0	8.0	0.0	8.0	4.0	0.5000	0.5000	0.1000	0.047
18.0	4.0	0.0	4.0	4.0	1.0000	0.0000	0.0000	0.000

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 10.50

2.25:

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
4.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
6.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
8.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.9250	0.042
10.0	37.0	0.0	37.0	1.0	0.0270	0.9730	0.9000	0.047
12.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.9000	0.047
14.0	36.0	0.0	36.0	1.0	0.0278	0.9722	0.8750	0.052
16.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
18.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.8500	0.056
20.0	34.0	0.0	34.0	1.0	0.0294	0.9706	0.8250	0.060
22.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250	0.060
24.0+	33.0	32.0	17.0	1.0	0.0588	0.9412	0.7765	0.074

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, ON MEDIUM RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9750	0.025
4.0	39.0	0.0	39.0	1.0	0.0256	0.9744	0.9500	0.034
6.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9500	0.034
8.0	38.0	0.0	38.0	3.0	0.0789	0.9211	0.8750	0.052
10.0	35.0	0.0	35.0	3.0	0.0857	0.9143	0.8000	0.063
12.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
14.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000	0.063
16.0	32.0	0.0	32.0	3.0	0.0938	0.9063	0.7250	0.071
18.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
20.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.7000	0.072
22.0	28.0	0.0	28.0	2.0	0.0714	0.9286	0.6500	0.075
24.0+	26.0	24.0	14.0	2.0	0.1429	0.8571	0.5571	0.089

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE FOR STRAIN A, ON LOW RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
4.0	40.0	0.0	40.0	5.0	0.1250	0.8750	0.8750	0.052
6.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
8.0	35.0	0.0	35.0	3.0	0.0857	0.9143	0.8000	0.063
10.0	32.0	0.0	32.0	3.0	0.0938	0.9063	0.7250	0.071
12.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
14.0	29.0	0.0	29.0	4.0	0.1379	0.8621	0.6250	0.077
16.0	25.0	0.0	25.0	3.0	0.1200	0.8800	0.5500	0.079
18.0	22.0	0.0	22.0	3.0	0.1364	0.8636	0.4750	0.079
20.0	19.0	0.0	19.0	0.0	0.0000	1.0000	0.4750	0.079
22.0	19.0	0.0	19.0	0.0	0.0000	1.0000	0.4750	0.079
24.0+	19.0	18.0	10.0	1.0	0.1000	0.9000	0.4275	0.084

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 19.33

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
4.0	38.0	0.0	38.0	3.0	0.0789	0.9211	0.8750	0.052
6.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
8.0	35.0	0.0	35.0	4.0	0.1143	0.8857	0.7750	0.066
10.0	31.0	0.0	31.0	2.0	0.0645	0.9355	0.7250	0.071
12.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.7250	0.071
14.0	29.0	0.0	29.0	2.0	0.0690	0.9310	0.6750	0.074
16.0	27.0	0.0	27.0	8.0	0.2963	0.7037	0.4750	0.079
18.0	19.0	0.0	19.0	13.0	0.6842	0.3158	0.1500	0.056
20.0	6.0	0.0	6.0	4.0	0.6667	0.3333	0.0500	0.034
22.0	2.0	0.0	2.0	1.0	0.5000	0.5000	0.0250	0.025
24.0+	1.0	0.0	1.0	1.0	1.0000	0.0000	0.0000	0.000

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 17.75

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
4.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9750	0.025
6.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.9750	0.025
8.0	39.0	0.0	39.0	2.0	0.0513	0.9487	0.9250	0.042
10.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.042
12.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.042
14.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.042
16.0	37.0	0.0	37.0	2.0	0.0541	0.9459	0.8750	0.052
18.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
20.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
22.0	35.0	0.0	35.0	2.0	0.0571	0.9429	0.8250	0.060
24.0+	33.0	33.0	16.5	0.0	0.0000	1.0000	0.8250	0.060

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, ON MEDIUM RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.00
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.00
4.0	40.0	0.0	40.0	3.0	0.0750	0.9250	0.9250	0.04
6.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.04
8.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250	0.04
10.0	37.0	0.0	37.0	1.0	0.0270	0.9730	0.9000	0.04
12.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.9000	0.04
14.0	36.0	0.0	36.0	3.0	0.0833	0.9167	0.8250	0.06
16.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250	0.06
18.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250	0.06
20.0	33.0	0.0	33.0	7.0	0.2121	0.7879	0.6500	0.07
22.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.6500	0.07
24.0+	26.0	25.0	13.5	1.0	0.0741	0.9259	0.6019	0.084

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, ON LOW RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
4.0	40.0	0.0	40.0	5.0	0.1250	0.8750	0.8750	0.052
6.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
8.0	35.0	0.0	35.0	5.0	0.1429	0.8571	0.7500	0.068
10.0	30.0	0.0	30.0	2.0	0.0667	0.9333	0.7000	0.072
12.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
14.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
16.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
18.0	28.0	0.0	28.0	2.0	0.0714	0.9286	0.6500	0.075
20.0	26.0	0.0	26.0	2.0	0.0769	0.9231	0.6000	0.07
22.0	24.0	0.0	24.0	3.0	0.1250	0.8750	0.5250	0.079
24.0+	21.0	21.0	10.5	0.0	0.0000	1.0000	0.5250	0.079

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.9500	0.034
4.0	38.0	0.0	38.0	3.0	0.0789	0.9211	0.8750	0.052
6.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750	0.052
8.0	35.0	0.0	35.0	5.0	0.1429	0.8571	0.7500	0.068
10.0	30.0	0.0	30.0	2.0	0.0667	0.9333	0.7000	0.072
12.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000	0.072
14.0	28.0	0.0	28.0	4.0	0.1429	0.8571	0.6000	0.07
16.0	24.0	0.0	24.0	5.0	0.2083	0.7917	0.4750	0.079
18.0	19.0	0.0	19.0	12.0	0.6316	0.3684	0.1750	0.060
20.0	7.0	0.0	7.0	2.0	0.2857	0.7143	0.1250	0.052
22.0	5.0	0.0	5.0	2.0	0.4000	0.6000	0.0750	0.042
24.0+	3.0	3.0	1.5	0.0	0.0000	1.0000	0.0750	0.042

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 17.60

LIFE TABLE FOR STRAIN A ADULTS, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
2.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9750
4.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.9750
6.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.9750
8.0	39.0	0.0	39.0	1.0	0.0256	0.9744	0.9500
10.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.9250
12.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250
14.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250
16.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250
18.0	37.0	0.0	37.0	5.0	0.1351	0.8649	0.8000
20.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000
22.0	32.0	0.0	32.0	3.0	0.0938	0.9063	0.7250
24.0+	29.0	29.0	14.5	0.0	0.0000	1.0000	0.7250

THE MEDIUM SURVIVAL TIMEFOR THIS DATA IS

LIFE TABLE FOR STRAIN A ADULTS, MEDIUM RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
2.0	40.0	0.0	40.0	3.0	0.0750	0.9250	0.9250
4.0	37.0	0.0	37.0	2.0	0.0541	0.9459	0.8750
6.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750
8.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.8500
10.0	34.0	0.0	34.0	1.0	0.0294	0.9706	0.8250
12.0	33.0	0.0	33.0	0.0	0.0000	1.0000	0.8250
14.0	33.0	0.0	33.0	3.0	0.0909	0.9091	0.7500
16.0	30.0	0.0	30.0	1.0	0.0333	0.9667	0.7250
18.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.7000
20.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.7000
22.0	28.0	0.0	28.0	8.0	0.2857	0.7143	0.5000
24.0+	20.0	20.0	10.0	0.0	0.0000	1.0000	0.5000

THE MEDIUM SURVIVAL TIME FOR THIS DATA IS

LIFE TABLE STRAIN A ADULTS, LOW RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
4.0	40.0	0.0	40.0	6.0	0.1500	0.8500	0.8500
6.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.8500
8.0	34.0	0.0	34.0	1.0	0.0294	0.9706	0.8250
10.0	33.0	0.0	33.0	2.0	0.0606	0.9394	0.7750
12.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.7750
14.0	31.0	0.0	31.0	2.0	0.0645	0.9355	0.7250
16.0	29.0	0.0	29.0	3.0	0.1034	0.8966	0.6500
18.0	26.0	0.0	26.0	3.0	0.1154	0.8846	0.5750
20.0	23.0	0.0	23.0	5.0	0.2174	0.7826	0.4500
22.0	18.0	0.0	18.0	0.0	0.0000	1.0000	0.4500
24.0+	18.0	18.0	9.0	0.0	0.0000	1.0000	0.4500

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 21.20

LIFE TABLE STRAIN A ADULTS STARVED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
4.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9750
6.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.9750
8.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.9750
10.0	39.0	0.0	39.0	4.0	0.1026	0.8974	0.8750
12.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750
14.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750
16.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8750
18.0	35.0	0.0	35.0	4.0	0.1143	0.8857	0.7750
20.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.7750
22.0	31.0	0.0	31.0	1.0	0.0323	0.9677	0.7500
24.0+	30.0	30.0	15.0	0.0	0.0000	1.0000	0.7500

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE STRAIN C ADULTS, FED

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	45.0	0.0	45.0	0.0	0.0000	1.0000	1.0000
2.0	45.0	0.0	45.0	0.0	0.0000	1.0000	1.0000
4.0	45.0	0.0	45.0	1.0	0.0222	0.9778	0.9778
6.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.9778
8.0	44.0	0.0	44.0	1.0	0.0227	0.9773	0.9556
10.0	43.0	0.0	43.0	0.0	0.0000	1.0000	0.9556
12.0	43.0	0.0	43.0	0.0	0.0000	1.0000	0.9556
14.0	43.0	0.0	43.0	3.0	0.0698	0.9302	0.8889
16.0	40.0	0.0	40.0	0.0	0.0000	1.0000	0.8889
18.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.8667
20.0	39.0	0.0	39.0	2.0	0.0513	0.9487	0.8222
22.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.8222
24.0+	37.0	36.0	19.0	1.0	0.0526	0.9474	0.7789

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE STARIN C ADULTS, MEDIUM RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000
2.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000
4.0	43.0	0.0	43.0	2.0	0.0465	0.9535	0.9535
6.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.9535
8.0	41.0	0.0	41.0	1.0	0.0244	0.9756	0.9302
10.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.9070
12.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.9070
14.0	39.0	0.0	39.0	4.0	0.1026	0.8974	0.8140
16.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.8140
18.0	35.0	0.0	35.0	3.0	0.0857	0.9143	0.7442
20.0	32.0	0.0	32.0	1.0	0.0313	0.9688	0.7209
22.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.7209
24.0+	31.0	30.0	16.0	1.0	0.0625	0.9375	0.6759

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE STRAIN C ADULTS, LOW RATION

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	41.0	0.0	41.0	0.0	0.0000	1.0000	1.0000
2.0	41.0	0.0	41.0	3.0	0.0732	0.9268	0.9268
4.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9268
6.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9268
8.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.9268
10.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.9024
12.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9024
14.0	37.0	0.0	37.0	6.0	0.1622	0.8378	0.7561
16.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.7561
18.0	31.0	0.0	31.0	2.0	0.0645	0.9355	0.7073
20.0	29.0	0.0	29.0	3.0	0.1034	0.8966	0.6341
22.0	26.0	0.0	26.0	2.0	0.0769	0.9231	0.5854
24.0+	24.0	24.0	12.0	0.0	0.0000	1.0000	0.5854

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

LIFE TABLE STRAIN C ADULTS STARVED
SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
2.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000
4.0	40.0	0.0	40.0	3.0	0.0750	0.9250	0.9250
6.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.9250
8.0	37.0	0.0	37.0	4.0	0.1081	0.8919	0.8250
10.0	33.0	0.0	33.0	1.0	0.0303	0.9697	0.8000
12.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000
14.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.8000
16.0	32.0	0.0	32.0	1.0	0.0313	0.9688	0.7750
18.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.7750
20.0	31.0	0.0	31.0	4.0	0.1290	0.8710	0.6750
22.0	27.0	0.0	27.0	4.0	0.1481	0.8519	0.5750
24.0+	23.0	13.0	16.5	10.0	0.6061	0.3939	0.2265

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 24.00+

2.3 Chapter4:

2.31:LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, CONTROL (0%SW)

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	14.0	0.3500	0.6500	0.6500	0.075
2.0	36.0	0.0	36.0	3.0	0.1154	0.8846	0.5750	0.078
3.0	33.0	0.0	33.0	6.0	0.2609	0.7391	0.4250	0.078
4.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.4250	0.078
5.0	27.0	0.0	27.0	1.0	0.0588	0.9412	0.4000	0.077
6.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.4000	0.077
7.0	26.0	0.0	26.0	1.0	0.0625	0.9375	0.3750	0.077
8.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.3750	0.077
9.0	25.0	0.0	25.0	1.0	0.0667	0.9333	0.3500	0.075
10.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.3500	0.075
11.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.3500	0.075
12.0	24.0	0.0	24.0	2.0	0.1429	0.8571	0.3000	0.072
13.0	22.0	0.0	22.0	1.0	0.0833	0.9167	0.2750	0.071
14.0	21.0	0.0	21.0	0.0	0.0000	1.0000	0.2750	0.071
15.0	21.0	0.0	21.0	0.0	0.0000	1.0000	0.2750	0.071
16.0	21.0	0.0	21.0	1.0	0.0909	0.9091	0.2500	0.068
17.0	20.0	0.0	20.0	0.0	0.0000	1.0000	0.2500	0.068
18.0	20.0	0.0	20.0	1.0	0.1000	0.9000	0.2250	0.066
19.0	19.0	0.0	19.0	0.0	0.0000	1.0000	0.2250	0.066
20.0	19.0	19.0	14.5	0.0	0.0000	1.0000	0.2250	0.066

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 3.50

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, 5%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	15.0	0.3000	0.7000	0.7000	0.065
2.0	35.0	0.0	35.0	6.0	0.1714	0.8286	0.5800	0.070
3.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
4.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.5600	0.070
5.0	28.0	0.0	28.0	2.0	0.0714	0.9286	0.5200	0.071
6.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.5200	0.071
7.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.5200	0.071
8.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.5200	0.071
9.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.5200	0.071
10.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.5200	0.071
11.0	26.0	0.0	26.0	1.0	0.0385	0.9615	0.5000	0.071
12.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
13.0	25.0	0.0	25.0	2.0	0.0800	0.9200	0.4600	0.070
14.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
15.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
16.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
17.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
18.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
19.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
20.0	23.0	23.0	11.5	0.0	0.0000	1.0000	0.4600	0.070

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 13.00

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, 10%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	13.0	0.2600	0.7400	0.7400	0.062
2.0	37.0	0.0	37.0	6.0	0.1622	0.8378	0.6200	0.069
3.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
4.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
5.0	31.0	0.0	31.0	1.0	0.0323	0.9677	0.6000	0.069
6.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
7.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
8.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
9.0	30.0	0.0	30.0	1.0	0.0333	0.9667	0.5800	0.070
10.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.5600	0.070
11.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
12.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
13.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
14.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
15.0	28.0	0.0	28.0	4.0	0.1429	0.8571	0.4800	0.071
16.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.4800	0.071
17.0	24.0	0.0	24.0	0.0	0.0000	1.0000	0.4800	0.071
18.0	24.0	0.0	24.0	1.0	0.0417	0.9583	0.4600	0.070
19.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
20.0	23.0	23.0	11.5	0.0	0.0000	1.0000	0.4600	0.070

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 15.75

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, 20%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	14.0	0.2800	0.7200	0.7200	0.063
2.0	36.0	0.0	36.0	4.0	0.1111	0.8889	0.6400	0.068
3.0	32.0	0.0	32.0	2.0	0.0625	0.9375	0.6000	0.069
4.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
5.0	30.0	0.0	30.0	1.0	0.0333	0.9667	0.5800	0.070
6.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
7.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
8.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
9.0	29.0	0.0	29.0	8.0	0.2759	0.7241	0.4200	0.070
10.0	21.0	0.0	21.0	0.0	0.0000	1.0000	0.4200	0.070
11.0	21.0	0.0	21.0	1.0	0.0476	0.9524	0.4000	0.069
12.0	20.0	0.0	20.0	1.0	0.0500	0.9500	0.3800	0.069
13.0	19.0	0.0	19.0	0.0	0.0000	1.0000	0.3800	0.069
14.0	19.0	0.0	19.0	0.0	0.0000	1.0000	0.3800	0.069
15.0	19.0	0.0	19.0	4.0	0.2105	0.7895	0.3000	0.065
16.0	15.0	0.0	15.0	0.0	0.0000	1.0000	0.3000	0.065
17.0	15.0	0.0	15.0	0.0	0.0000	1.0000	0.3000	0.065
18.0	15.0	0.0	15.0	5.0	0.3333	0.6667	0.2000	0.057
19.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2000	0.057
20.0	10.0	10.0	5.0	0.0	0.0000	1.0000	0.2000	0.057

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 9.50

LIFE TABLE FOR STRAIN A, NEWLY RELEASED JUVENILES, 40%

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	51.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	51.0	0.0	50.0	33.0	0.6471	0.3529	0.3529	0.067
2.0	18.0	0.0	18.0	1.0	0.0556	0.9444	0.3333	0.066
3.0	17.0	0.0	17.0	5.0	0.2941	0.7059	0.2353	0.059
4.0	12.0	0.0	12.0	1.0	0.0833	0.9167	0.2157	0.058
5.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2157	0.058
6.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2157	0.058
7.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2157	0.058
8.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2157	0.058
9.0	11.0	0.0	11.0	1.0	0.0909	0.9091	0.1961	0.056
10.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.1765	0.053
11.0	9.0	0.0	9.0	2.0	0.2222	0.7778	0.1373	0.048
12.0	7.0	0.0	7.0	0.0	0.0000	1.0000	0.1373	0.048
13.0	7.0	0.0	7.0	0.0	0.0000	1.0000	0.1373	0.048
14.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
15.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
16.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
17.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
18.0	31.0	0.0	31.0	2.0	0.0645	0.9355	0.5800	0.070
19.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
20.0	29.0	29.0	14.5	0.0	0.0000	1.0000	0.5800	0.070

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, CONTROL (0%SW)

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	47.0	0.0	47.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	47.0	0.0	47.0	2.0	0.0541	0.9459	0.9459	0.037
2.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
3.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
4.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
5.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
6.0	45.0	0.0	45.0	2.0	0.0571	0.9429	0.8919	0.051
7.0	43.0	0.0	43.0	0.0	0.0000	1.0000	0.8919	0.051
8.0	43.0	0.0	43.0	2.0	0.0606	0.9394	0.8378	0.061
9.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8378	0.061
10.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8378	0.061
11.0	41.0	0.0	41.0	2.0	0.0645	0.9355	0.7838	0.068
12.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.7838	0.068
13.0	39.0	0.0	39.0	2.0	0.0690	0.9310	0.7297	0.073
14.0	37.0	3.0	35.5	0.0	0.0000	1.0000	0.7297	0.073
15.0	34.0	2.0	33.0	0.0	0.0000	1.0000	0.7297	0.073
16.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.7297	0.073
17.0	32.0	2.0	31.0	0.0	0.0000	1.0000	0.7297	0.073
18.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.7297	0.073
19.0	30.0	2.0	29.0	18.0	0.9474	0.0526	0.0384	0.038

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 19.33

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, 5%SW
SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	15.0	0.3000	0.7000	0.7000	0.065
2.0	35.0	0.0	35.0	5.0	0.1429	0.8571	0.6000	0.069
3.0	30.0	0.0	30.0	1.0	0.0333	0.9667	0.5800	0.070
4.0	29.0	0.0	29.0	1.0	0.0345	0.9655	0.5600	0.070
5.0	28.0	0.0	28.0	5.0	0.1786	0.8214	0.4600	0.070
6.0	23.0	0.0	23.0	0.0	0.0000	1.0000	0.4600	0.070
7.0	23.0	0.0	23.0	1.0	0.0435	0.9565	0.4400	0.070
8.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.4400	0.070
9.0	22.0	0.0	22.0	3.0	0.1364	0.8636	0.3800	0.069
10.0	19.0	0.0	19.0	7.0	0.3684	0.6316	0.2400	0.060
11.0	12.0	0.0	12.0	0.0	0.0000	1.0000	0.2400	0.060
12.0	12.0	0.0	12.0	0.0	0.0000	1.0000	0.2400	0.060
13.0	12.0	0.0	12.0	1.0	0.0833	0.9167	0.2200	0.059
14.0	11.0	0.0	11.0	1.0	0.0909	0.9091	0.2000	0.057
15.0	10.0	0.0	10.0	0.0	0.0000	1.0000	0.2000	0.057
16.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.1800	0.054
17.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
18.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
19.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
20.0	9.0	9.0	4.5	0.0	0.0000	1.0000	0.1800	0.054

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 5.60

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, 10%SW
SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	17.0	0.3400	0.6600	0.6600	0.067
2.0	33.0	0.0	33.0	6.0	0.1818	0.8182	0.5400	0.070
3.0	27.0	0.0	27.0	6.0	0.2222	0.7778	0.4200	0.070
4.0	21.0	0.0	21.0	3.0	0.1429	0.8571	0.3600	0.068
5.0	18.0	0.0	18.0	0.0	0.0000	1.0000	0.3600	0.068
6.0	18.0	0.0	18.0	7.0	0.3889	0.6111	0.2200	0.059
7.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2200	0.059
8.0	11.0	0.0	11.0	0.0	0.0000	1.0000	0.2200	0.059
9.0	11.0	0.0	11.0	1.0	0.0909	0.9091	0.2000	0.057
10.0	10.0	0.0	10.0	1.0	0.1000	0.9000	0.1800	0.054
11.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
12.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
13.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
14.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
15.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
16.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
17.0	9.0	0.0	9.0	0.0	0.0000	1.0000	0.1800	0.054
18.0	9.0	0.0	9.0	1.0	0.1111	0.8889	0.1600	0.052
19.0	8.0	0.0	8.0	0.0	0.0000	1.0000	0.1600	0.052
20.0	8.0	8.0	4.0	0.0	0.0000	1.0000	0.1600	0.052

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 3.33

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, 20%SW
SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	22.0	0.4400	0.5600	0.5600	0.070
2.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
3.0	28.0	0.0	28.0	3.0	0.1071	0.8929	0.5000	0.071
4.0	25.0	0.0	25.0	4.0	0.1600	0.8400	0.4200	0.070
5.0	21.0	0.0	21.0	3.0	0.1429	0.8571	0.3600	0.068
6.0	18.0	0.0	18.0	3.0	0.1667	0.8333	0.3000	0.065
7.0	15.0	0.0	15.0	0.0	0.0000	1.0000	0.3000	0.065
8.0	15.0	0.0	15.0	0.0	0.0000	1.0000	0.3000	0.065
9.0	15.0	0.0	15.0	9.0	0.6000	0.4000	0.1200	0.046
10.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
11.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
12.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
13.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
14.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
15.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
16.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
17.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
18.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
19.0	6.0	0.0	6.0	0.0	0.0000	1.0000	0.1200	0.046
20.0	6.0	6.0	3.0	0.0	0.0000	1.0000	0.1200	0.046

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 4.0

LIFE TABLE FOR STRAIN C, NEWLY RELEASED JUVENILES, 40%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	59.0	0.0	59.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	59.0	0.0	59.0	31.0	0.5254	0.4746	0.4746	0.065
2.0	28.0	0.0	28.0	6.0	0.2143	0.7857	0.3729	0.063
3.0	22.0	0.0	22.0	1.0	0.0455	0.9545	0.3559	0.062
4.0	21.0	0.0	21.0	3.0	0.1429	0.8571	0.3051	0.060
5.0	18.0	0.0	18.0	4.0	0.2222	0.7778	0.2373	0.055
6.0	14.0	0.0	14.0	4.0	0.2857	0.7143	0.1695	0.049
7.0	10.0	0.0	10.0	10.0	1.0000	0.0000	0.0000	0.000

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 1.95

2.32

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, CONTROL (0%SW)

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	4.0	0.1000	0.9000	0.9000	0.047
2.0	46.0	0.0	46.0	2.0	0.0556	0.9444	0.8500	0.056
3.0	44.0	0.0	44.0	1.0	0.0294	0.9706	0.8250	0.060
4.0	43.0	0.0	43.0	0.0	0.0000	1.0000	0.8250	0.060
5.0	43.0	0.0	43.0	3.0	0.0909	0.9091	0.7500	0.068
6.0	40.0	0.0	40.0	0.0	0.0000	1.0000	0.7500	0.068
7.0	40.0	0.0	40.0	1.0	0.0333	0.9667	0.7250	0.071
8.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.7250	0.071
9.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.7250	0.071
10.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.7250	0.071
11.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.7250	0.071
12.0	39.0	0.0	39.0	1.0	0.0345	0.9655	0.7000	0.072
13.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7000	0.072
14.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7000	0.072
15.0	38.0	0.0	38.0	1.0	0.0357	0.9643	0.6750	0.074
16.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.6750	0.074
17.0	37.0	0.0	37.0	1.0	0.0370	0.9630	0.6500	0.075
18.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.6500	0.075
19.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.6500	0.075
20.0	36.0	36.0	13.0	0.0	0.0000	1.0000	0.6500	0.075

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, 5%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	2.0	0.0400	0.9600	0.9600	0.028
2.0	48.0	0.0	48.0	2.0	0.0417	0.9583	0.9200	0.038
3.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
4.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
5.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
6.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
7.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
8.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
9.0	46.0	0.0	46.0	0.0	0.0000	1.0000	0.9200	0.038
10.0	46.0	0.0	46.0	4.0	0.0870	0.9130	0.8400	0.052
11.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8400	0.052
12.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8400	0.052
13.0	42.0	0.0	42.0	7.0	0.1667	0.8333	0.7000	0.065
14.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
15.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
16.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
17.0	35.0	0.0	35.0	4.0	0.1143	0.8857	0.6200	0.069
18.0	31.0	0.0	31.0	1.0	0.0323	0.9677	0.6000	0.069
19.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
20.0	30.0	30.0	15.0	0.0	0.0000	1.0000	0.6000	0.069

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, 10%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	3.0	0.0600	0.9400	0.9400	0.034
2.0	47.0	0.0	47.0	9.0	0.1915	0.8085	0.7600	0.060
3.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
4.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
5.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
6.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
7.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
8.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
9.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
10.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.7400	0.062
11.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7400	0.062
12.0	37.0	0.0	37.0	1.0	0.0270	0.9730	0.7200	0.063
13.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
14.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
15.0	36.0	0.0	36.0	4.0	0.1111	0.8889	0.6400	0.068
16.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.6400	0.068
17.0	32.0	0.0	32.0	2.0	0.0625	0.9375	0.6000	0.069
18.0	30.0	0.0	30.0	4.0	0.1333	0.8667	0.5200	0.071
19.0	26.0	0.0	26.0	0.0	0.0000	1.0000	0.5200	0.071
20.0	26.0	26.0	13.0	0.0	0.0000	1.0000	0.5200	0.071

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, 20%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	3.0	0.0600	0.9400	0.9400	0.034
2.0	47.0	0.0	47.0	6.0	0.1277	0.8723	0.8200	0.054
3.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8200	0.054
4.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8200	0.054
5.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8200	0.054
6.0	41.0	0.0	41.0	3.0	0.0732	0.9268	0.7600	0.060
7.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
8.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7600	0.060
9.0	38.0	0.0	38.0	2.0	0.0526	0.9474	0.7200	0.063
10.0	36.0	0.0	36.0	1.0	0.0278	0.9722	0.7000	0.065
11.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
12.0	35.0	0.0	35.0	2.0	0.0571	0.9429	0.6600	0.067
13.0	33.0	0.0	33.0	1.0	0.0303	0.9697	0.6400	0.068
14.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.6400	0.068
15.0	32.0	0.0	32.0	4.0	0.1250	0.8750	0.5600	0.070
16.0	28.0	0.0	28.0	3.0	0.1071	0.8929	0.5000	0.071
17.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
18.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
19.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
20.0	25.0	25.0	12.5	0.0	0.0000	1.0000	0.5000	0.071

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 17.00

LIFE TABLE FOR STRAIN A, LARGE JUVENILES, 40%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	10.0	0.2000	0.8000	0.8000	0.057
2.0	40.0	0.0	40.0	4.0	0.1000	0.9000	0.7200	0.063
3.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
4.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
5.0	36.0	0.0	36.0	1.0	0.0278	0.9722	0.7000	0.065
6.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.6800	0.066
7.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
8.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
9.0	34.0	0.0	34.0	3.0	0.0882	0.9118	0.6200	0.069
10.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
11.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
12.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
13.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
14.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
15.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
16.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
17.0	31.0	0.0	31.0	0.0	0.0000	1.0000	0.6200	0.069
18.0	31.0	0.0	31.0	2.0	0.0645	0.9355	0.5800	0.070
19.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
20.0	29.0	29.0	14.5	0.0	0.0000	1.0000	0.5800	0.070

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, CONTROL (0%SW)

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	47.0	0.0	47.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	47.0	0.0	47.0	2.0	0.0541	0.9459	0.9459	0.037
2.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
3.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
4.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
5.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9459	0.037
6.0	45.0	0.0	45.0	2.0	0.0571	0.9429	0.8919	0.051
7.0	43.0	0.0	43.0	0.0	0.0000	1.0000	0.8919	0.051
8.0	43.0	0.0	43.0	2.0	0.0606	0.9394	0.8378	0.061
9.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8378	0.061
10.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8378	0.061
11.0	41.0	0.0	41.0	2.0	0.0645	0.9355	0.7838	0.068
12.0	39.0	0.0	39.0	0.0	0.0000	1.0000	0.7838	0.068
13.0	39.0	0.0	39.0	2.0	0.0690	0.9310	0.7297	0.073
14.0	37.0	3.0	35.5	0.0	0.0000	1.0000	0.7297	0.073
15.0	34.0	2.0	33.0	0.0	0.0000	1.0000	0.7297	0.073
16.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.7297	0.073
17.0	32.0	2.0	31.0	0.0	0.0000	1.0000	0.7297	0.073
18.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.7297	0.073
19.0	30.0	2.0	29.0	18.0	0.9474	0.0526	0.0384	0.038

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 19.33

LIFE TABLE FOR STRAIN C, LARGE JUVENILES,5%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	50.0	2.0	49.0	0.0	0.0000	1.0000	1.0000	0.000
3.0	48.0	0.0	48.0	0.0	0.0000	1.0000	1.0000	0.000
4.0	48.0	0.0	48.0	0.0	0.0000	1.0000	1.0000	0.000
5.0	48.0	2.0	47.0	0.0	0.0000	1.0000	1.0000	0.000
6.0	46.0	0.0	46.0	0.0	0.0000	1.0000	1.0000	0.000
7.0	46.0	0.0	46.0	0.0	0.0000	1.0000	1.0000	0.000
8.0	46.0	0.0	46.0	0.0	0.0000	1.0000	1.0000	0.000
9.0	46.0	0.0	46.0	0.0	0.0000	1.0000	1.0000	0.000
10.0	46.0	0.0	46.0	0.0	0.0000	1.0000	1.0000	0.000
11.0	46.0	9.0	41.5	0.0	0.0000	1.0000	1.0000	0.000
12.0	37.0	0.0	37.0	0.0	0.0000	1.0000	1.0000	0.000
13.0	37.0	4.0	35.0	0.0	0.0000	1.0000	1.0000	0.000
14.0	33.0	0.0	33.0	0.0	0.0000	1.0000	1.0000	0.000
15.0	33.0	0.0	33.0	0.0	0.0000	1.0000	1.0000	0.000
16.0	33.0	0.0	33.0	0.0	0.0000	1.0000	1.0000	0.000
17.0	33.0	0.0	33.0	0.0	0.0000	1.0000	1.0000	0.000
18.0	33.0	0.0	33.0	0.0	0.0000	1.0000	1.0000	0.000
19.0	33.0	33.0	16.5	0.0	0.0000	1.0000	1.0000	0.000

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 19.00+

LIFE TABLE FOR STRAIN C, LARGE JUVENILES, 10%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	5.0	47.5	0.0	0.0000	1.0000	1.0000	0.000
2.0	45.0	2.0	44.0	0.0	0.0000	1.0000	1.0000	0.000
3.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
4.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
5.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
6.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
7.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
8.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
9.0	43.0	0.0	43.0	0.0	0.0000	1.0000	1.0000	0.000
10.0	43.0	2.0	42.0	0.0	0.0000	1.0000	1.0000	0.000
11.0	41.0	0.0	41.0	0.0	0.0000	1.0000	1.0000	0.000
12.0	41.0	1.0	40.5	0.0	0.0000	1.0000	1.0000	0.000
13.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
14.0	40.0	0.0	40.0	0.0	0.0000	1.0000	1.0000	0.000
15.0	40.0	6.0	37.0	0.0	0.0000	1.0000	1.0000	0.000
16.0	34.0	0.0	34.0	0.0	0.0000	1.0000	1.0000	0.000
17.0	34.0	0.0	34.0	0.0	0.0000	1.0000	1.0000	0.000
18.0	34.0	1.0	33.5	0.0	0.0000	1.0000	1.0000	0.000
19.0	33.0	1.0	32.5	32.0	0.9846	0.0154	0.0154	0.022

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 19.51

LIFE TABLE FOR STRAIN C 20%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	3.0	48.5	0.0	0.0000	1.0000	1.0000	0.000
2.0	47.0	0.0	47.0	6.0	0.1277	0.8723	0.8723	0.049
3.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8723	0.049
4.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8723	0.049
5.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8723	0.049
6.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8723	0.049
7.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8723	0.049
8.0	41.0	0.0	41.0	0.0	0.0000	1.0000	0.8723	0.049
9.0	41.0	0.0	41.0	3.0	0.0732	0.9268	0.8085	0.05
10.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.8085	0.05
11.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.8085	0.05
12.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.7872	0.06
13.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
14.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
15.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
16.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
17.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
18.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
19.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7872	0.06
20.0	37.0	37.0	18.5	0.0	0.0000	1.0000	0.7872	0.06

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN C, 40%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	7.0	0.1400	0.8600	0.8600	0.049
2.0	43.0	0.0	43.0	6.0	0.1395	0.8605	0.7400	0.062
3.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7400	0.062
4.0	37.0	0.0	37.0	1.0	0.0270	0.9730	0.7200	0.063
5.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
6.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
7.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
8.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
9.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.7200	0.063
10.0	36.0	0.0	36.0	1.0	0.0278	0.9722	0.7000	0.065
11.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
12.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.6800	0.066
13.0	34.0	0.0	34.0	1.0	0.0294	0.9706	0.6600	0.067
14.0	33.0	0.0	33.0	1.0	0.0303	0.9697	0.6400	0.068
15.0	32.0	0.0	32.0	2.0	0.0625	0.9375	0.6000	0.069
16.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
17.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
18.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
19.0	30.0	0.0	30.0	0.0	0.0000	1.0000	0.6000	0.069
20.0	30.0	30.0	15.0	0.0	0.0000	1.0000	0.6000	0.069

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00

2.33:

LIFE TABLE FOR STRAIN A, ADULTS, CONTROL (0%SW)

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	3.0	0.0750	0.9250	0.9250	0.042
2.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9250	0.042
3.0	47.0	0.0	47.0	3.0	0.0811	0.9189	0.8500	0.056
4.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.8500	0.056
5.0	44.0	0.0	44.0	2.0	0.0588	0.9412	0.8000	0.063
6.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8000	0.063
7.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8000	0.063
8.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8000	0.063
9.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8000	0.063
10.0	42.0	0.0	42.0	0.0	0.0000	1.0000	0.8000	0.063
11.0	42.0	0.0	42.0	2.0	0.0625	0.9375	0.7500	0.068
12.0	40.0	0.0	40.0	2.0	0.0667	0.9333	0.7000	0.072
13.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7000	0.072
14.0	38.0	0.0	38.0	0.0	0.0000	1.0000	0.7000	0.072
15.0	38.0	0.0	38.0	2.0	0.0714	0.9286	0.6500	0.075
16.0	36.0	0.0	36.0	0.0	0.0000	1.0000	0.6500	0.075
17.0	36.0	0.0	36.0	7.0	0.2692	0.7308	0.4750	0.079
18.0	29.0	0.0	29.0	2.0	0.1053	0.8947	0.4250	0.078
19.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.4250	0.078
20.0	27.0	27.0	8.5	0.0	0.0000	1.0000	0.4250	0.078

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 17.86

LIFE TABLE FOR STRAIN A, ADULTS, 5%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	1.0	0.0200	0.9800	0.9800	0.020
2.0	49.0	0.0	49.0	2.0	0.0408	0.9592	0.9400	0.034
3.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
4.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
5.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
6.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
7.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
8.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
9.0	47.0	0.0	47.0	4.0	0.0851	0.9149	0.8600	0.049
10.0	43.0	0.0	43.0	8.0	0.1860	0.8140	0.7000	0.065
11.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
12.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
13.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
14.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
15.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
16.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
17.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
18.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
19.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
20.0	35.0	35.0	17.5	0.0	0.0000	1.0000	0.7000	0.065

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN A, ADULTS,10%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	4.0	0.0800	0.9200	0.9200	0.038
2.0	46.0	0.0	46.0	1.0	0.0217	0.9783	0.9000	0.042
3.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	0.042
4.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	0.042
5.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	0.042
6.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	0.042
7.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	0.042
8.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	0.042
9.0	45.0	0.0	45.0	2.0	0.0444	0.9556	0.8600	0.049
10.0	43.0	0.0	43.0	5.0	0.1163	0.8837	0.7600	0.060
11.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.7400	0.062
12.0	37.0	0.0	37.0	9.0	0.2432	0.7568	0.5600	0.070
13.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
14.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
15.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
16.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
17.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
18.0	28.0	0.0	28.0	0.0	0.0000	1.0000	0.5600	0.070
19.0	28.0	0.0	28.0	2.0	0.0714	0.9286	0.5200	0.071
20.0	26.0	26.0	13.0	0.0	0.0000	1.0000	0.5200	0.071

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN A, ADULTS, 20%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	1.0	0.0200	0.9800	0.9800	0.020
2.0	49.0	0.0	49.0	0.0	0.0000	1.0000	0.9800	0.020
3.0	49.0	0.0	49.0	2.0	0.0408	0.9592	0.9400	0.033
4.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
5.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.033
6.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
7.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.033
8.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
9.0	47.0	0.0	47.0	1.0	0.0213	0.9787	0.9200	0.039
10.0	46.0	0.0	46.0	6.0	0.1304	0.8696	0.8000	0.057
11.0	40.0	0.0	40.0	4.0	0.1000	0.9000	0.7200	0.063
12.0	36.0	0.0	36.0	4.0	0.1111	0.8889	0.6400	0.068
13.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.6400	0.068
14.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.6400	0.068
15.0	32.0	0.0	32.0	7.0	0.2188	0.7813	0.5000	0.071
16.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
17.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
18.0	25.0	0.0	25.0	2.0	0.0800	0.9200	0.4600	0.070
19.0	23.0	0.0	23.0	1.0	0.0435	0.9565	0.4400	0.070
20.0	22.0	22.0	11.0	0.0	0.0000	1.0000	0.4400	0.070

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 18.00

LIFE TABLE FOR STRAIN A, ADULTS, 40%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	
1.0	50.0	0.0	50.0	3.0	0.0600	0.9400	0.9400	
2.0	47.0	0.0	47.0	2.0	0.0426	0.9574	0.9000	
3.0	45.0	0.0	45.0	0.0	0.0000	1.0000	0.9000	
4.0	45.0	0.0	45.0	2.0	0.0444	0.9556	0.8600	
5.0	43.0	0.0	43.0	3.0	0.0698	0.9302	0.8000	
6.0	40.0	0.0	40.0	0.0	0.0000	1.0000	0.8000	
7.0	40.0	0.0	40.0	0.0	0.0000	1.0000	0.8000	
8.0	40.0	0.0	40.0	0.0	0.0000	1.0000	0.8000	
9.0	40.0	0.0	40.0	2.0	0.0500	0.9500	0.7600	
10.0	38.0	0.0	38.0	9.0	0.2368	0.7632	0.5800	
11.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	
12.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	
13.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	

LIFE TABLE (CONTD)

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
14.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800
15.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800
16.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800
17.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800
18.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800
19.0	29.0	0.0	29.0	3.0	0.1034	0.8966	0.5200
20.0	26.0	26.0	13.0	0.0	0.0000	1.0000	0.5200

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN C, ADULTS, CONTROL (0%SW)

SURVIVAL VARIABLE WEEK

	INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
2.0	50.0	0.0	50.0	2.0	0.0500	0.9500	0.9500	0.034
3.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
4.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
5.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
6.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
7.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
8.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
9.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
10.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
11.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
12.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
13.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
14.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
15.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
16.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
17.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
18.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
19.0	48.0	0.0	48.0	0.0	0.0000	1.0000	0.9500	0.034
20.0	48.0	48.0	29.0	0.0	0.0000	1.0000	0.9500	0.034

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN C, ADULTS, 5%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	2.0	0.0400	0.9600	0.9600	0.028
2.0	48.0	0.0	48.0	1.0	0.0208	0.9792	0.9400	0.034
3.0	47.0	0.0	47.0	0.0	0.0000	1.0000	0.9400	0.034
4.0	47.0	0.0	47.0	1.0	0.0213	0.9787	0.9200	0.038
5.0	46.0	0.0	46.0	1.0	0.0217	0.9783	0.9000	0.042
6.0	45.0	0.0	45.0	1.0	0.0222	0.9778	0.8800	0.046
7.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.8800	0.046
8.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.8800	0.046
9.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.8800	0.046
10.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.8800	0.046
11.0	44.0	0.0	44.0	0.0	0.0000	1.0000	0.8800	0.046
12.0	44.0	0.0	44.0	3.0	0.0682	0.9318	0.8200	0.054
13.0	41.0	0.0	41.0	7.0	0.1707	0.8293	0.6800	0.066
14.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
15.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
16.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
17.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
18.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
19.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
20.0	34.0	34.0	17.0	0.0	0.0000	1.0000	0.6800	0.066

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

LIFE TABLE FOR STRAIN C, ADULTS, 10%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	2.0	0.0400	0.9600	0.9600	0.028
2.0	48.0	0.0	48.0	8.0	0.1667	0.8333	0.8000	0.057
3.0	40.0	0.0	40.0	5.0	0.1250	0.8750	0.7000	0.065
4.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
5.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
6.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.6800	0.066
7.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
8.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
9.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
10.0	34.0	0.0	34.0	5.0	0.1471	0.8529	0.5800	0.070
11.0	29.0	0.0	29.0	0.0	0.0000	1.0000	0.5800	0.070
12.0	29.0	0.0	29.0	2.0	0.0690	0.9310	0.5400	0.070
13.0	27.0	0.0	27.0	0.0	0.0000	1.0000	0.5400	0.070
14.0	27.0	0.0	27.0	6.0	0.2222	0.7778	0.4200	0.070
15.0	21.0	0.0	21.0	5.0	0.2381	0.7619	0.3200	0.066
16.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.3200	0.066
17.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.3200	0.066
18.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.3200	0.066
19.0	16.0	0.0	16.0	0.0	0.0000	1.0000	0.3200	0.066
20.0	16.0	16.0	8.0	0.0	0.0000	1.0000	0.3200	0.066

LIFE TABLE FOR STRAIN C, ADULTS, 20%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	CUMUL SE OF SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	3.0	0.0600	0.9400	0.9400	0.034
2.0	47.0	0.0	47.0	12.0	0.2553	0.7447	0.7000	0.065
3.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
4.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.6800	0.066
5.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
6.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
7.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
8.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
9.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
10.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
11.0	34.0	0.0	34.0	2.0	0.0588	0.9412	0.6400	0.068
12.0	32.0	0.0	32.0	7.0	0.2188	0.7813	0.5000	0.071
13.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
14.0	25.0	0.0	25.0	0.0	0.0000	1.0000	0.5000	0.071
15.0	25.0	0.0	25.0	3.0	0.1200	0.8800	0.4400	0.070
16.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.4400	0.070
17.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.4400	0.070
18.0	22.0	0.0	22.0	0.0	0.0000	1.0000	0.4400	0.070
19.0	22.0	0.0	22.0	3.0	0.1364	0.8636	0.3800	0.069
20.0	19.0	19.0	9.5	0.0	0.0000	1.0000	0.3800	0.069
0.000								

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 15.00

LIFE TABLE FOR STRAIN C, ADULTS, 40%SW

SURVIVAL VARIABLE WEEK

INTVL START TIME	NUMBER ENTRNG THIS INTVL	NUMBER WDRAWN DURING INTVL	NUMBER EXPOSD TO RISK	NUMBER OF TERMNL EVENTS	PROPN TERMI-NATING	PROPN SURVI-VING	CUMUL PROPN SURV AT END	SE OF CUMUL SURV-IVING
0.0	50.0	0.0	50.0	0.0	0.0000	1.0000	1.0000	0.000
1.0	50.0	0.0	50.0	6.0	0.1200	0.8800	0.8800	0.046
2.0	44.0	0.0	44.0	4.0	0.0909	0.9091	0.8000	0.057
3.0	40.0	0.0	40.0	1.0	0.0250	0.9750	0.7800	0.059
4.0	39.0	0.0	39.0	1.0	0.0256	0.9744	0.7600	0.060
5.0	38.0	0.0	38.0	1.0	0.0263	0.9737	0.7400	0.062
6.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7400	0.062
7.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7400	0.062
8.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7400	0.062
9.0	37.0	0.0	37.0	0.0	0.0000	1.0000	0.7400	0.062
10.0	37.0	0.0	37.0	2.0	0.0541	0.9459	0.7000	0.065
11.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
12.0	35.0	0.0	35.0	0.0	0.0000	1.0000	0.7000	0.065
13.0	35.0	0.0	35.0	1.0	0.0286	0.9714	0.6800	0.066
14.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
15.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
16.0	34.0	0.0	34.0	0.0	0.0000	1.0000	0.6800	0.066
17.0	34.0	0.0	34.0	2.0	0.0588	0.9412	0.6400	0.068
18.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.6400	0.068
19.0	32.0	0.0	32.0	0.0	0.0000	1.0000	0.6400	0.068
20.0	32.0	32.0	16.0	0.0	0.0000	1.0000	0.6400	0.068

THE MEDIAN SURVIVAL TIME FOR THESE DATA IS 20.00+

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