STUDIES ON THE INFLUENCE OF TOTAL DISSOLVED SOLIDS ON THE BIOLOGY OF CERTAIN FRESHWATER MOLLUSCS

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ABSTRACT

Life tables were compiled for cohorts of Bulinus (Physopsis) globosus (Morelet), Biomphalaria pfeifferi (Krauss), Bulinus (Bulinus) tropicus (Krauss) and Lymnaea natalensis Krauss at constant conductivities of 125, 180, 250, 310, 375, 500, 625, 750, 875 and 1 000 µS. Life tables were also compiled for B. salinarum (Morelet) and B. (P.) africanus (Krauss) at 900 µS. Adaptation and acclimatization by the same and successive generations to conditions that were thought to be unfavourable were studied with the aid of life tables.

Four species were simultaneously kept in each experimental situation where one aquarium was used for each different conductivity. The species were isolated from each other in the aquaria by keeping them in separate perlon gauze containers. A drip feed recirculation system was used to supply water to the aquaria. The temperature of the water in the aquaria was controlled at a constant temperature of 25°C and various physical and chemical properties of the water were monitored at regular intervals.

From the life tables the net reproductive rate (R_o), the mean cohort generation time (T), the innate capacity for increase (r_m), the capacity for increase (r_c) and the finite rate of increase (λ) were calculated.

From the range of r_m values as such it was concluded that total dissolved solids at the values occurring in their permanent natural habitats has no profound effect on the biology of B. pfeifferi and B. (P.) globosus whereas the distribution of L. natalensis seems to be restricted by values giving conductivities higher than 375 µS and that of B. (B.) tropicus by conductivities lower than ± 180 µS. In all four the above species the total dissolved solids has a greater effect on the egg and juvenile stages than on the adult snails and it is mainly as a result of this that the total effect of this factor on snails is manifested. The optimum value of total dissolved solids for both B. salinarum and B. (P.) africanus appeared to be higher than was expected.

The possible influence of total dissolved solids on the geographic distribution and habitat selection of the freshwater snails investigated is discussed.

CONTENTS

1. INTRODUCTION

It is generally acknowledged that the conditions prevailing in the freshwater environment are the result of the combined action of a complex of biotic and abiotic factors. These factors often affect each other mutually and affect the inhabitants of this biotope in various ways. It is therefore clear that the suitability of a habitat for colonization by organisms is determined by the interaction of these factors which are therefore collectively and individually responsible for the distribution and abundance of freshwater organisms. In the natural habitat it is often very difficult if not impossible to evaluate the importance of any single factor especially as it is known that many of the conditioning factors fluctuate within a wide range. As a result of which a wide ecological amplitude is of vital importance for the survival of freshwater organisms.

The extensive distribution and abundance of freshwater snails in practically any freshwater habitat is undeniably proof of their generally euryok nature and particular potential to survive practically any ecological situation. Despite their wide tolerance range for most ecological factors, situations do occur where one or more factors exceed the normal values and thereby also the tolerance limits of the snails and although they possess survival mechanisms (e.g. aestivation) such catastrophies invariably result in the total eradication of the vulnerable snails from the habitat.

One of the important abiotic factors conditioning the freshwater biotope is undoubtedly the quality of the water and in particular its chemical composition which is known to have a profound affect on the snails living therein (WHO, 1956). However, very little is known regarding the exact nature of the effect of this factor on the snails. As a rule chemical factors may act in two ways. Deficiency of supply of certain essential elements may limit life in a habit while an excess of certain elements may have a deleterious effect on the snails especially when lethal concentrations of such substances are reached. A thorough knowledge of the tolerance ranges as well as the optimum requirements regarding the chemical composition of the water is therefore of obvious importance. This information is invaluable both where artificial conditions for the culture of snails are to be created and where the suitability of an area such as a new irrigation scheme, is being assessed for possible future colonization by snails.

The importance of the effect of dissolved minerals on the snails has been recognised and investigated by a great many authors who, unfortunately, still disagree on this matter. Helmy (1953), Marill (1953), Alves (1958), De Meillon, Frank & Allanson (1958), Deschiens (1954 & 1957) and Schutte & Frank (1964) could find no, or very little indication of any correlation between snail distribution and the chemical properties of the natural waters. It is not unlikely that this could be attributed to the fact that the chemical composition of the waters investigated by these authors fell within the tolerance ranges of the snails because evidence that the chemical composition of the water does generally affect the snails in various ways has been recorded by Van Someren (1946), Vermeil, Tournoux, Tocheport, Noger & Schmitt (1952), De Azevedo, Cambournac & Pinto (1954), Deschiens (1954), Litalien & Deschiens (1954), Dechange & Deschiens (1955), Alves (1956), Abdel-Malek (1958), Harrison, Nduku & Hooper (1966), Harrison (1968), Harrison, Williams & Greig (1970), Williams (1970a & b), Liang (1971), Lo (1972) and Jennings, De Kock & Van Eeden (1973). More specifically in this respect, Zavattari (1938), Watson (1953 & 1958) and Mandahl-Barth, Malaisse & Ripert (1972) maintain that high salinities very definitely affect especially the distribution of snails adversely. A shortage of certain essential elements in the water also is harmful to the snails and according to Mozley (1944), Harry & Cumbie (1956a & b), Harry, Cumbie & Martinez de Jesus (1957), Harry & Aldrich (1958) and Pimentel & White (1959) it particularly affects the distribution, fecundity, and growth. In many cases the role played by the chemical composition of the water is deduced from casual observations made in the course of routine ecological surveys so that very little exact data on this subject is available. The investigations of Harrison et al. (1970), Williams (1970b) and Jennings et al. (1973) are notable exceptions in this respect in so far as they quantitatively assessed the responses of *Biomphalaria pfeifferi* (Krauss) to dissolved minerals in the water by studying certain aspects of its population dynamics. Williams (1970b) also included *Bulinus (Physopsis) globosus* (Morelet) in his investigations.

The objective of the present study was to establish accurately the responses of *B. pfeifferi*, *B.(P.) globosus*, *Lymnaea natalensis* Krauss and *Bulinus (Bulinus) tropicus* (Krauss) to waters with various mineral concentrations using electrical conductivity as an index of the mineral concentration of the water. All the species investigated in this study are known to act as intermediate hosts of certain human and animal trematode parasites and their responses were assessed in terms of population dynamics based on life tables. Particular importance was attached to the biometric statistic, the intrinsic rate of natural increase (r_m).

2. MATERIAL AND METHODS

2.1 Breeding equipment and procedures

A primary requisite for the successful breeding of freshwater snails under carefully controlled laboratory conditions is a well planned functional maintenance unit. As, in the course of time, the requirements of the snails became better understood the containers in which they were kept by investigators varied according to the requirements and objectives of the investigation in which they were being used. For short term experiments a reasonable measure of success had been obtained with dishes and bowls by Wright (1960), McClelland (1964), Sturrock (1965), Storey (1970) and Coles (1973). Trays were found successful by McClelland (1964), jars by Colton & Pennypacker (1934) and DeWitt (1967) and glass tanks and aquaria satisfied Cole (1925), Standen (1951), Chernin & Michelson (1957a & b), Cridland (1958), Frank (1963), Garnett (1964), Shiff (1964a & b), Shiff (1966), Demian & Ibrahim (1972), Eveland & Ritchie (1972) and Thomas & Benjamin (1974a).

In an attempt to create near optimal artificial conditions for the snails, however, a system of re-circulating water has proven to have a great many advantages and the use of this type of system has been recommended by Swart & Reinecke (1962), Ritchie, Berrios-Duran & De Weese (1963), Prinsloo (1966), Van der Steen (1968), Bruce & Radke (1971), De Kock (1973) and Van der Schalie & Berry (1973). In spite of high initial expense in constructing such a system it offers several advantages which offset this expense. The most important single advantage of this system is the fact that the re-circulation of a large volume of water makes it possible to maintain large numbers of snails in relatively small aquaria. Further advantages are described in detail by Ritchie et al. (1963) and De Kock (1973).

Consequently the basic design of the re-circulating system described by Prinsloo (1966) and De Kock (1973) was used in the present study, but a few minor alterations which are regarded as improvements were included. The simultaneous testing of more than one type of water necessitated the construction of four separate systems. Each system, however, made use of only one single large aquarium.

The four rectangular aquaria (45 x 45 x 15 cm) with a capacity 28 350 cm^3 were manufactured from 1mm thick stainless steel sheeting and each was suspended in a stainless steel water bath (65 x 55 x 20 cm) with a capacity of 39 575 cm^3. The water baths were insulated by means of double sides with layers of glass fibre between them. The larger overall dimensions of

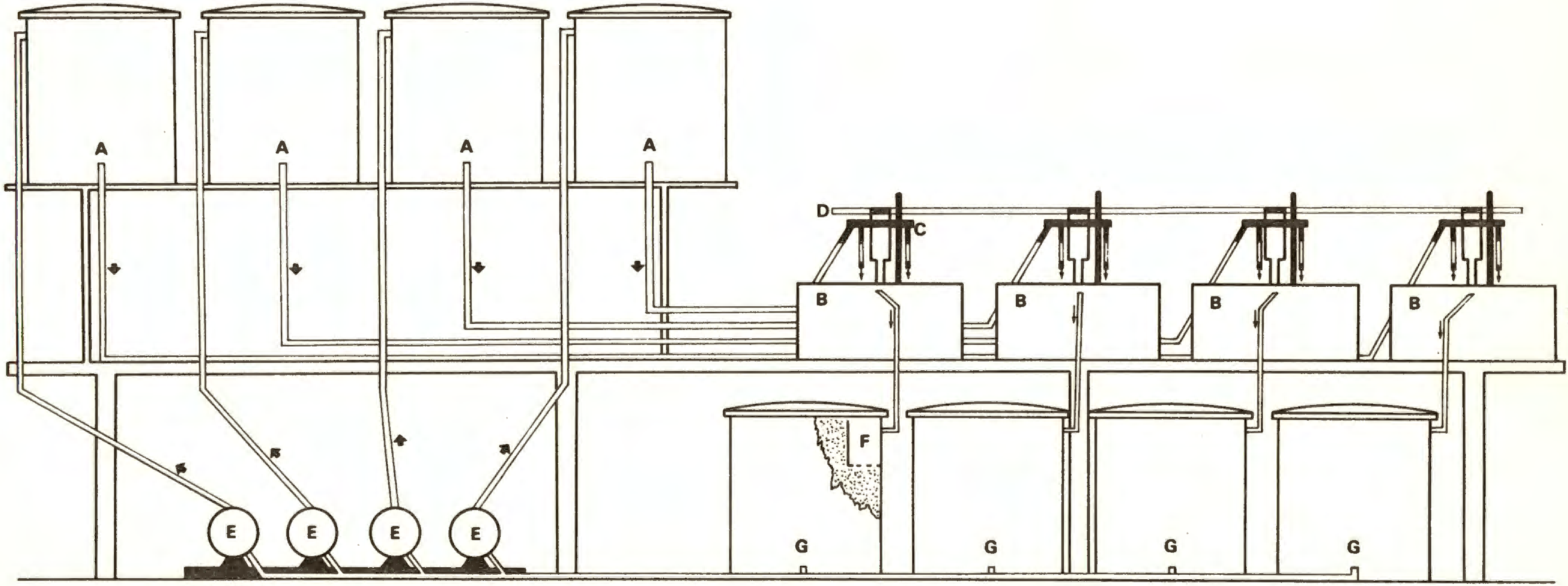

Figure I. Diagrammatic representation of the experimental lay-out

A - Overhead reservoirs
B - Aquaria
C - Overhead water distributors
D - Suspension rod
E - Centrifugal pumps
F - Activated charcoal filter
G - Reservoirs

these aquaria had more than double the capacity of those used by Prinsloo (1960) and De Kock (1973) and made it possible to experiment with four species simultaneously in the same aquarium. This obviously shortened the experimental period.

The lay-out of the system is illustrated in figure 1 and plates 1 and 2. Water was supplied to each aquarium by means of an overhead four pronged distributor which delivered four separate drips into the aquarium. The volume of the four drips was regulated to displace 5 000 cm^3 of water per hour from each aquarium. An overflow drain pipe was fitted to each aquarium and this regulated the level and volume of water. Water was supplied to the distributors from four polythene reservoirs, each with a capacity of 120 000 cm^3. The reservoirs were positioned 1,5 metres above the aquaria and consequently the feed was gravitational.

The overflow drains delivered the displaced water to four iden=tical polythene tanks on the floor underneath the aquaria. Before entering these tanks the water was passed through an activated charcoal and biological filter. The function of the charcoal filter will be discussed in detail later on. The water in the floor tanks was pumped back into the overhead re=servoirs by means of four centrifugal pumps, each controlled by an automatic sump switch in the floor tank which started the pumps as soon as the water reached a certain level in these tanks. The volume of water in circulation was exactly enough to fill one overhead reservoir and one aquarium. More than this was never circulated, as a precautionary measure in case of possible power failures etc., in which case the volume of water in circulation would only fill the floor tank and never overflow it. This did away with the electro-magnetic valves used in the systems of Prinsloo (1966) and De Kock (1973).


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The temperature of the water in the water baths was regulated by Lauda ultra thermostats As precise temperature control was not one of the objects of this experiment the ultra thermostats were not connected to a cooling system. The temperatures consequently fluctuated slightly.

The snails were accommodated in two different types of containers. Initially the eggs and hatchlings were kept in PVC rings (10 x 5 cm) with gauze bottoms made from perlon thread 40µ thick and with a mesh of 45µ. The permeability of this guaze was 28%.

At an age of two weeks the snails were transferred to larger PVC rings (15 x 10 cm) also with gauze bottoms. The perlon thread used for these bottoms had a diameter of 200µ, a mesh of 375µ and a permeability of 43%.

Four rings were suspended in an aquarium, each under a drip. The use of loose containers suspended in the aquaria was initiated by De Kock (1973). The snails were transferred to clean containers every morning. This allowed the quick removal of egg clutches and cleaning of aquaria without unduly disturbing the snails because removing egg clutches from loose containers that can be lifted out of the aquarium is accomplished quicker and easier than removing them from the sides and bottoms of aquaria full of water.

The specific conductivity of a solution is, according to the I.B.P. Handbook No. 8, a measure of its capacity to convey an electrical current. This is the sum of the conductivities of the individual species of positive and negative ions since the conductivity of an ion is determined partly by its mobility in the electric field and since this mobility depends on the temperature, the conductivity of a solution also depends on the temperature. The conductivity furthermore depends on the concentration and the degree of ionization of the salts involved. It, however, gives no indication of the nature of the substances in solution but any increase or decrease in their concentrations will be reflected in a concomittant increase or decrease in conductivity. The conductivity of most freshwaters is so low that it is customary to express it as micro Siemens/centimetre (µS).

South African freshwaters display a wide range of conductivities. De Meillon, et al. (1958) measured conductivities ranging from 37 to 475 µS in the Crocodile and Klein Jukskei Rivers and according to Schutte & Frank (1964) the waters of the South-eastern Transvaal and Northern Swaziland gave readings varying between 24 and 1 500 µS. De Kock & Van Eeden (1969) recorded conductivities of 110 to 830 µS in the Mooi River (Transvaal) while the conductivities of the water in the Loskop Dam listed by Mulder, Kruger & Van Eeden (1970) varied between 105 and 220 µS. It was accordingly, decided to conduct the present experiment within these ranges in an attempt to establish a possible relationship between the experimental and natural situation.

Eleven culture waters with different conductivities were made up with the aid of a WTW electrode type conductivity meter. The following conductivities were prepared: 50, 125, 180, 250, 310, 375, 500, 625, 750, 875 and 1 000 µS. Borehole water with a conductivity of 600 µS was used as stock water for the preparation of the culture waters. For all conductivities below 600 µS the borehole water was diluted with distilled water until the required conductivity was obtained. Conductivities higher than 600 µS were obtained by allowing the borehole water to evaporate from large open containers. Due to the large demand for water this process had to be speeded up by raising the temperature of the water in these open containers to 60°C. In this way it was possible to concentrate the salts present in the water and conductivities of up to 2 000 µS were reached. The water was left to age for at least a week before it was used in the system of circulating water. The loss of water due to evaporation from the aquaria was compensated for by the addition of distilled water. It was possible to control the conductivity of the water in the systems fairly accurately and no fluctuation of more than ± 5 μS ever occurred.

A perusal of the results of Shiff (1964a), Sturrock (1966), Prinsloo (1966), Shiff & Garnett (1967), Sturrock & Sturrock (1972) and De Kock (1973) reveals that the optimum temperature for growth and reproduction of a great many freshwater snail species lies somewhere between 20 and 30°C. Different species have different optimum temperature requirements and since the species were to be kept together during this experiment, a temperature had to be selected which, although not optimal for all the species concerned, had to be at least acceptable to all four. It was consequently decided to experiment at 25°C. One advantage of working at this temperature was that conductivities could be directly determined in the aquaria because at this temperature no compensation for the influence of temperature on conductivity is neccessary.

The crowding phenomenon is the most frequently discussed subject where the rearing of snails under artificial conditions is concerned. Although it is now generally accepted that overcrowding exercises a deleterious effect on growth and natality no unanimity exists either as to the exact cause of the observed ill effects or the nature of these effects. DeWitt (1954) describes a decline in the shell size of *Physa gyrina* Say as well as a reduction in mean egg production per snail with increasing numbers of snails. Chernin & Michelson (1957a & b) blame increasing population density of *Australorbis glabratus* (Say) (=*Biomphalaria glabrata* (Say)) for declining numbers of egg clutches/snail, eggs/snail and eggs/clutch. Specimens in numerically smaller populations also displayed higher growth rates. In a follow-up investigation these two authors found that a 50% reduction in the water volume in which snails were kept had less of a detrimental effect on their results than a doubling of the number of snails in the original volume of water. Apparently crowding due to a reduction in area is less harmful than crowding due to an increase in population size. These authors ascribe the ill effects of crowding to increased physical contact between snails with increased mutual interference.

De Kock (1973) on the other hand found that four cohorts of 50 specimens each of *B.(B.) tropicus* reached higher total egg productions than two cohorts of 35 specimens of *B.(B.) tropicus* under identical conditions in aquaria of the same size. De Kock (1973) maintains that the size of the container in which the snails are kept is of no importance providing the volume of water in circulation is adequate and the food, oxygen and hygienic requirements of the snails are met. This point of view is also shared by Boray (1964) and Eisenberg (1966).

Noland & Carriker (1946) found overcrowding of *Lymnaea stagnalis appressa* Say to be decidedly detrimental to the extent and rate of growth, the number of snails that reach optimum size, condition of the shell etc.

According to Wright (1960) no single factor can alone be blamed for the effects of population density on growth and reproduction and he suggested that at least one of the factors responsible for this in his studies on *Bulinus (Bulinus) forskali* (Ehrenberg) was the presence of a pheromone in the culture medium. The existence of such a toxin has subsequently been discovered by Berrie & Visser (1963) working with *Biomphalaria sudanica* (Martens) and by Levy, Tunis & Isseroff (1973) who experimented with *Fossaria cubensis*. Wright (1960) found it possible to isolate this toxin from the culture water by filtering the water through an activated charcoal layer while Berrie & Visser (1963) maintain that it can be destroyed by aerating the water and thereby oxidizing it.

Apparently population density can be increased to a certain level without any untoward effect on the snails. On the contrary some findings seem to suggest that this activity has a beneficial ef=

fect on their growth and maturation rates. This phenomenon of increased growth and maturation rates resulting from increasing population density up to a critical threshold is known as the Allee effect (Thomas & Benjamin, 1974a & b and Thomas, Goldsworthy & Benjamin, 1974). This, in essence, is what Chernin & Michelson (1957a & b) observed with *B. glabrata*. The Allee effect is not unique to snails. It has been reported to operate in a variety of other organisms including small rodents, birds, insects, crustaceans and bacterial populations.

Cohorts of a practical size which does not influence the reliability of the results is essential where sixteen cohorts are being used simultaneously. Various authors investigating the influence of ecological and other factors on snails have used varying cohort sizes. Shiff (1964a), studying the effect of temperature on *B. globosus* used 34 to 48 snails per cohort while Sturrock (1966) used 91 to 111 specimens of *B. pfeifferi* per cohort for similar studies. Prinsloo (1966) worked with 35 specimens each of *L. natalensis* and *B.(B.) tropicus* per cohort.

During an investigation of the influence of water soluble substances on the egg production of *L. natalensis* and *B.(B.) tropicus* Ackermann (1972) statistically established the permissibility of a minimum of 20 snails per cohort. De Kock (1973) determined the experimental error committed when calculating r_m on the performance of limited numbers of snails per cohort. He obtained a difference of 0,058 between the r_m values calculated from cohorts of 20 and 200 specimens each. This error was considered permissible for the present investigation and accordingly only 20 snails per cohort were used, giving a total of 80 snails per aquarium.

The total volume of water in circulation in each system was 148 350 cm^3 thus allowing 1 854,375 cm^3 per snail. This ratio was considered adequate for the normal requirements of the snails and is considerably higher than both the 681,6327 cm^3/snail of

De Kock (1973) and the ratios allowed by the authors listed in table 1.

TABLE 1.

Volumes of water in which various authors bred snails

Author	Species	cm^3/snail
Wright, 1960	*B.(B.) forskali*	40
Berrie & Visser, 1963	*B. sudanica*	25
Frank, 1963	*B. pfeifferi*	50
Garnett, 1964	*B.(P.) globosus*	66
	B. pfeifferi	50
	L. natalensis	1 000
McClelland, 1964	*B.(P.) nasutus*	125-150

Additionally 30 000 cm^3 of water was replaced from each system every week.

Aeration of the water in which snails are being kept has become a common practice. The importance of maintaining an adequate and efficient supply of air into the culture waters is stressed by Standen (1948), Chernin & Michelson (1957a & b), Cridland (1958), Timmermans (1959), Swart & Reinecke (1962), Shiff (1966), Bruce & Radke (1971), Demian & Ibrahim (1972), Lo (1972), Calow (1973) De Kock (1973), Van der Schalie & Berry (1973) and Thomas & Benjamin (1974a). All these authors accomplished aeration with the aid of compressor pumps. Aeration can also be accomplished by the introduction of plants into the aquaria as suggested by Noland & Carriker (1946), Standen (1951), Timmermans (1959) and McClelland (1964), but Noland & Carriker (1946) regard the presence of plants as unnecessary when artificial aeration is practiced. Apart from the fact that the efficient production of oxygen by plants is dependent on sufficient light reaching the plants, they also hamper the removal of egg clutches.

There are various important reasons for maintaining a high oxygen tension in the water. It has been established by Noland & Carriker (1946), McGraw (1952), Vaughn (1953) and Swart & Reinecke (1962) that insufficiently aerated egg clutches hatch either poorly or not at all. Abdel-Malek's (1956) statement that snails are more dependent on dissolved oxygen than on atmospheric oxygen was experimentally confirmed by Alberts (1966) who indicated that in *B.(P.) africanus*, *B.(B.) tropicus* and *L. natalensis* cutaneous respiration exceeds pulmonary respiration in importance. The oxygen carrying capacity of water decreases with rising temperature, so much so that Alberts (1966) found cutaneous respiration to increase by as much as 288% when the temperature of the water increased from 15°-25°C. This makes the continual aeration of water at 25°C essential to prevent the mass mortalities encountered by this author. According to Van Someren (1946) *L. cailaudi* showed signs of stress at 70-80% oxygen saturation and died when this value reached 10%. Certain species, however, are not very sensitive to the oxygen tension in the water. Frank (1964) considers a 55% saturation as adequate for both *B.(P.) africanus* and *B. pfeifferi* and is of opinion that these species are only under stress when the value drops below 30%. That *Bulinus (B.) tropicus* is well adapted to living under practically anoxic conditions is testified by Van Aardt's (1972) findings that it's haemoglobin is capable of saturating it's oxygen carrying capacity at a 1% saturation level of the surrounding water. In the event of snails having to revert to pulmonary respiration they would be forced to regularly acsend to the surface for oxygen and this, according to De Kock (1973), would constitute a continual interruption of their reproductive and feeding processes. According to Timmermans (1959) the oxygen concentration of the water also influences the oviposition of *Planorbis corneus* Linnaeus, *Planorbis planorbis* Linnaeus, *Physa acuta* Draparnaud, and *Lymnaea stagnalis* (Linnaeus).

Aeration has the further advantages of preventing the formation of a bacterial film on the surface of the water by the creation of turbulence in the aquaria as well as keeping putrefaction of fecal material and waste food to a minimum. DeWitt (1954a) prevented the build up of metabolic wastes by aerating the aquaria in which he kept specimens of *P. gyrina*. This proce= dure was also followed by Frank (1968) for controlling metabolic wastes in aquaria containing *B. pfeifferi* and Berrie & Visser (1963) report the destruction of the toxic pheromone isolated by them from an overpopulated habitat, by aeration. Each aquarium was therefore aerated individually with compressed air during the present investigation.

Hydrogen-ion concentration during the first couple of months of the experiment, was determined twice a week with the aid of an Orion Research model 701 digital pH meter. Although pH increased slightly in direct proportion to conductivity there was so little fluctuation in the pH of the individual systems that pH determinations were reduced to once a week. The very small increase in pH observed with rising conductivity was possibly caused by increasing $CaCO_3$ concentration (Table 2) called the alkali reserve by Welch (1952). It appears, how= ever, as if this rise was counteracted by a corresponding rise in SO_4^{2-} and the other elements which have a lowering effect on pH. The fact that plants which, according to Hubendick (1958), can cause pH fluctuations, were absent from the system, possibly contributed towards the very small fluctuation in pH that was observed.

Field and laboratory trials have revealed without exception that snail hosts of bilharziasis tolerate a wide range of pH values and according to Deschiens (1956) and Abdel-Malek (1958) pH is seldom a limiting factor in their distribution. This is also true for *L. caillaudi* (Van Someren, 1946).

De Azevedo et al. (1954) recorded the following pH ranges in Mozambique: *B.(P.) africanus* and *B. pfeifferi* habitats : 6,0 - 8,2; *B.(B.) forskali* habitats: 6,6 - 7,2. In Fezzan Vermeil et al. (1952) found *Bulinus (Bulinus)* sp. in waters with a pH range of 7,1 - 8,0 while Deschiens (1954) experimentally determined the pH tolerance of *Bulinus (Bulinus) truncatus* (Audouin) and *Bulinus (Bulinus) contortus* (Michaud) to lie between 4,5 and 10. In the freshwater snail habitat of the Transvaal Lowveld Schutte & Frank (1964) measured pH values ranging from below 6,7 to above 8,4 while De Meillon et al. (1958) recorded values between 7 and 8,2 in High and Lowveld rivers.

While, therefore, most species appear to be tolerant of a wide range of pH values, it is not impossible that excessive acidity or alkalinity may act as a limiting factor, but such extremes are probably rare in natural waters. It can thus be reasonably assumed that the range of 8,2 - 8,6 obtained during this investigation was not unfavourable for the snails.

Dissolved oxygen and bio-chemical oxygen demand were determined twice weekly with the aid of WTW electrode type oxygen meter. Calculation of the percentage dissolved oxygen in the water was done with the aid of the I.B.P. Handbook No. 8. The bio-chemical oxygen demand was measured by incubating the water samples in the dark at 20°C for five days and then determining the ammount of oxygen used by oxidation during the incubation period.

The aeration of the different aquaria proved to be so successful that the water was practically always either 100% saturated with oxygen or very nearly so (Appendix Table 1-11). The oxygen determinations were therefore reduced to weekly intervals.
De Kock (1973) detected a drop in oxygen tension at the onset of egg production. This was also the case during this investigation but the aeration of the aquaria was correspondingly increased and it was thus possible to maintain a very high level of oxygen tension.

The bio-chemical oxygen demand (B.O.D.) fluctuated between 0 - 7,1 kg/m^3. The high values recorded during certain stages of the experiment indicated definite organic pollution of the water.

In contrast with this Prinsloo (1966) recorded a highest value of 11,6 kg/m^3 while De Kock (1973) obtained a highest B.O.D. value of 7,6 kg/m^3. The latter author noticed a gradual increase in B.O.D. values which he attributes to the increased food consumption and consequent increase in defecation which occurs during the reproductive period. Similar observations were made during this investigation. This trend was reversed as egg production decreased and mortality increased.

Different snail species reveal different degrees of tolerance towards pollution. According to Abdel-Malek (1958) a slight degree of organic pollution is favourable for certain Planorbidae. This seems to be in line with views expressed earlier on (WHO, 1956) that a certain degree of pollution by decaying organic matter and excrement is definitely favourable to the snails which transmit bilharziasis while chemical pollution appears to be almost invariably deleterious to these snail hosts. Frank (1963) found a slight degree of organic pollution favourable to *B. pfeifferi* and although De Meillon et al. (1958) found *B.(P.) africanus* unable to survive in sewage water with a high degree of pollution *B.(B.) tropicus*, in their opinion, showed no signs of distress in such water. De Kock & Van Eeden (1969) recovered *L. columella* and *B.(B.) tropicus* only from those parts of the Mooi River (Tvl) which were organically enriched whereas *L. natalensis* and *B.(P.) africanus* occurred only in the cleaner parts of the river. While Harry & Aldrich (1958) could not find any specimens of *B. glabrata* in polluted waters, *L. caillaudi* was restricted in its distribution to polluted waters (Van Someren, 1946). It does, therefore, seem as if pollution above a certain concentration constitutes a factor harmful to snails.

The biological and charcoal filters in the re-circulating systems as well as the replacement of water from the systems were measures to combat the effect of pollution on the snails in the experimental situation.

The chemical analysis of the eleven experimental culture water types as well as that of the habitat waters from which the parental snails were obtained, is presented in table 2. The influence of the various concentrations on the snails is discussed later.

Snails of which the progeny were used in this investigation were obtained from three sources. *Biomphalaria pfeifferi* and *B.(P.) globosus* were supplied by the Bilharzia Field Unit of the SAMRC from domesticated stocks at Nelspruit.

Lymnaea natalensis was collected from cement irrigation canals directly below the wall of Boskop Dam (grid reference 26.27 Ca) and *B.(B.) tropicus* from an earth dam on the Municipal Townlands (grid reference 26.27 Cc) of Potchefstroom.

Diet, obviously, is important for obtaining optimal growth and reproductive rates. In earlier investigations a number of diets were used with varying degrees of success. Lettuce, prepared in various ways has been used by Roney (1943), Cowper (1946), Noland & Carriker (1946), Cridland (1958), Claugher (1960), Wright (1960), Swart & Reinecke (1962), Garnett (1964) and Thomas & Benjamin (1974a) but Eveland & Ritchie (1972) maintain that it does not support maximum growth and reproductive rates and Ritchie et al. (1963) is of opinion that it does not appeal to the snails. To correct this deficiency, Pimentel (1957) supplemented lettuce with algae. McClelland (1964) added a manure extract, Frank (1963) lucern and Prinsloo (1966) both fecal material of snails and algae. None of these measures produced any obvious increase in the performance of the snails. A variety of other snail foods have also been tried by various authors such as Colton & Pennypacker (1934), Standen (1951), Cridland (1958), Ritchie et al. (1963) and Calow (1973), all of whom observed varying degrees of success. Many of these snail diets, however, cannot be utilized by very young snails.

Table 2

Analyses of waters used during the experiments as well as that of the waters from which the parental snails were obtained.

	Conductivity		50µS	125µS	180µS	250µS	310µS	375µS	500µS	625µS	750µS	875µS	1000µS	M_1	B_1	N_1
ppm	Sodium	(Na)	<4	<4	5	6	5	11	16	21	28	31	44	11	5	3
	Potassium	(K)	<0,4	0,5	0,6	1,6	1,8	1,8	2,6	4,1	4,6	4,4	4,5	3,8	1	1,7
	Calcium	(Ca)	3	6	7	13	14	10	18	19	11	7	3	23	16	22
	Magnesium	(Mg)	3	10	13	18	20	31	46	60	81	>100	>100	22	18	2
	Kjeldahl-nitrogen	(N)	<0,2	<0,2	0,2	0,2	<0,2	0,2	0,4	0,9	0,8	0,4	0,5	0,2	<0,2	0,60
	Ammonia-nitrogen	(N)	<0,2	<0,2	<0,2	←	<0,2				2	→	0,5	<0,2	<0,2	0,20
	Nitrate+nitrite-nitrogen	(N)	0,3	0,3	0,5	2,8	0,9	2,7	2,3	2,3	2,1	0,4	0,7	<0,2	0,3	<0,2
	Nitrite-nitrogen	(N)	<0,1	<0,1	<0,1	<0,1	<0,1	0,1	<0,1	0,2	0,2	<0,1	<0,1	<0,1	<0,1	<0,1
	Sulphate	(SO_4)	7	13	22	25	32	48	73	97	>100	>100	>100	23	19	18
	Total phosphate	(P)	<0,2	<0,2	<0,2	0,6	0,6	0,6	0,6	0,7	0,9	<0,2	<0,2	<0,2	<0,2	<0,2
	Orto-phosphate	(P)	<0,2	<0,2	<0,2	0,4	0,4	0,3	0,4	0,5	0,8	<0,2	<0,2	<0,2	<0,2	<0,2
	Chloride	(Cl)	<5	5	7	8	9	12	19	24	31	34	49	17	7	<5
	Total Alkalinity	($CaCO_3$)	18	41	54	74	79	94	149	179	203	305	296	131	97	48

M_1 - Habitat water of *B.(B.)tropicus*

B_1 - Habitat water of *L.natalensis*

N_1 - Habitat water of *B.pfeiferi* and *B.(P.)globosus*

In search of a suitable diet that would be acceptable to both young and adult snails, Jennings, De Kock & Van Eeden (1970) tested five different types of snail food on *B. pfeifferi*. These experiments showed "Tetramin Conditioning Food", a patented food for fish, to be ideally suited and this finding has since been confirmed by De Kock (1973) who used a mixture of "Tetramin Conditioning and Staple Food". It has also been used by Webbe & James (1971) with equally satisfying results and Coles (1973) testing a similar fish food called "Phillips Fish Food" which does not significantly differ from Tetramin, recorded excellent results. The fact that this food in powdered form is very well suited for hatchlings and juveniles adds to its usefulness. The snails used in this investigation were reared on a 50:50 mixture of "Tetramin Conditioning and Staple Foods". Hatchlings were fed finely powdered "Tetramin Conditioning Food".

Between 50 and 100 eggs laid during the same 24 hour period by the parental snails were placed in the small circular containers described earlier on. An accurate record of the exact number of eggs placed in each container was kept for the purpose of calculating the hatching percentage. The egg clutches were transferred to identical clean containers each morning until hatching commenced. Thereafter the hatchlings were transferred to identical clean containers every morning with the aid of a small paint brush. Parent snails were kept at 400 S in the laboratory.

When the snails were two weeks old they were placed into the larger circular containers with the larger mesh and the use of finely powdered "Tetramin Conditioning Food" was discontinued in favour of "Tetramin Staple and Conditioning Food" in flake form. A daily routine was established where the containers in which the snails were kept were changed and the snails put into clean containers. The dirty containers were then washed after all egg clutches had been removed from them. A daily record of egg production and mortality was kept.

The aquaria were drained and cleaned once a week and the water lost from the system was replenished.

Apart from this weekly replacement of water only distilled water was added from time to time to compensate for loss by evaporation.

Growth monitoring by means of mass is preferable to length measurements because, according to Thomas & Benjamin (1974a), it is more sensitive. The individual weighing of snails as done by Prinsloo (1966), Combrinck (1968) and Thomas & Benjamin (1974a) is too time consuming when experimenting with large numbers of snails. Consequently all the specimens of a cohort were weighed simultaneously, first at an age of two weeks and fortnightly thereafter.

This was done after the manner described by Jennings et al. (1970) and De Kock (1973). Twenty cm^3 of water was pipetted into a 50 cm^3 plastic container with a lid, and then weighed. The cohort of snails to be weighed was removed from their container and dried on filter paper. They were then placed in the weighed container with its 20 cm^3 of water and weighed. The difference between the two masses constitutes the mass of the cohort from which the mean mass increase per specimen was calculated.

The effect of mortalities on the growth rate is an important factor that should, for two reasons, always be kept in mind when growth rates are compared. Firstly the death of a single large specimen might result in the calculation of a mean mass per specimen which may be smaller than that which had been obtained a fortnight earlier. This would falsely suggest a negative growth. The death of a very small specimen would obviously have the opposite effect. Secondly every death reduces the population pressure in the cohort concerned and might therefore influence the living conditions for the survivors so that the real effect of the factor being evaluated becomes obscured. These effects of mortality on mass calculation were also experienced by De Kock (1973) and consequently any conclu= sions drawn from the growth rate curves become progressively less reliable as the cohort numbers decrease.

2.2 Population statistics

2.2.1 Life tables

One of the principal goals of ecologists, according to Collier, Cox, Johnson & Miller (1973), is to understand how natural pro= cesses determine the size and composition of plant and animal populations, eventually with enough thoroughness to be able to predict accurately changes in these variables from information on changes in environmental factors. Aspects of population ecology concerned with the description of population processes can be determined by using statistics such as birth, death and reproduction rates. Various population statistics are usually summarized in table form and referred to as a life table. The literature of ecology contains many examples of life tables from a great variety of taxonomic groups. The data is usually obtained by sampling a population under one set of environmen= tal conditions and it is a great advantage that it is usually possible to obtain such data experimentally. Life tables are used by ecologists to compare the responses of two or more ecologically similar species to the same environment or the re= sponses of one single species to different environmental situa= tions. Both these cases suggest a comparative approach in which several life tables are used and as such they have been employed in the study of freshwater snails by DeWitt (1954a), Shiff (1964a & b), Harrison & Shiff (1966), Prinsloo (1966), Shiff & Husting (1966), Sturrock (1966), Shiff & Garnett (1967), Sturrock & Sturrock (1970), Williams (1970b), Sturrock & Stur= rock (1972), De Kock (1973) and Jennings et al.(1973).

2.2.2 Survivorship (1_x)

Age specific death rate is defined as the quotient of the number of organisms of age x dying in a short interval of time divided by the number of age x that were alive at the start of that interval of time. The diminishment of a cohort through time can be shown by means of a curve known as a survivorship curve and the number of the cohort remaining alive at any particular age x is symbolized as 1_x and thus survivorship curves are commonly called 1_x curves. Thus while the first column in the life table shows the age x of the cohort for each time interval, the 1_x column shows how many individuals from the cohort are still alive at the beginning of the corresponding age interval. These values are adjusted to what they would be if the cohort had begun with 1,0000 individuals. This kind of adjustment has the advantage of simplifying comparisons of several life tables.

2.2.3 Natality (m_x age specific birth rate)

This is the average number of female offspring produced per unit time by a female in the age class x (Collier et al., 1973). In the case of the monoecious self fertilizing snails the birth of every individual has to be taken in account.

2.2.4 The egg curve ($1_x m_x = V_x$)

The products of 1 and m at each age, x, ($1_x m_x$, designated V_x by Laughlin, 1965) give the number of eggs laid in each unit of time with centre x. The products $1_x m_x$ can themselves be plotted against age x to give the egg curve (Laughlin, 1965) called the proportional egg curve by Combrinck (1968). This curve is the end product of survival and reproduction of the cohort under the conditions of the experiment.

With the aid of the data contained in the life tables the following statistics can be calculated:

2.2.5 The intrinsic rate of natural increase (r_m) and the capacity for increase (r_c)

A great deal of attention has been paid to the ability of animals to increase but no general agreement as to the definition thereof exists (Birch, 1948). Chapman (1921) refers to it as the biotic potential and Andrewartha & Birch (1954) suggested the term "innate capacity for increase". According to them this is the quantitative expression of the reproductive potential of a population growing in an invironment in which the quality of food, space and animals of the same kind are kept at an optimum level and other organisms of different kinds are excluded. Collier et al. (1973) suggest the use of the symbol r rather than the designation of any specific denomination for this function which they find to be misleading.

There is no simple equation for the calculation of r and the initial development in this respect was done by Lotka (1925) and Dublin & Lotka (1925) who called it the true, inherent or intrinsic rate of natural increase. They have shown that

$$\int_o^\infty e^{-rx} l_x m_x dx = 1 \qquad (1)$$

from which r_m can be calculated by numerical approximation techniques (Birch, 1948) using the following equation

$$\Sigma e^{-rx} l_x m_x = 1 \qquad (2)$$

Here x is taken to be the centre point of each age group and the summation is carried out over all age groups for which $m_x>0$. The whole process is greatly simplified by the use of four figure tables for powers of e. Since these tables only give values of $e^{\pm x}$ at intervals of 0,01 in the argument x up to $e^{\pm 6}$ it may be convenient to multiply both sides of the equation by a factor e^k in order to work with powers of e which lie in the more detailed parts of the table. Birch (1948), Watson (1964) and Southwood (1966) took k to be seven and the equation then appears as follows:

$$e^7 \Sigma e^{-r_m x} l_x m_x = e^7$$

$$\Sigma e^{7-r_m x} l_x m_x = 1\,096,6 \qquad (3)$$

Andrewartha & Birch (1954) describe two methods for the calculation of r_m; the one method being very accurate and the other a rough approximation. Laughlin (1965) proposes that the statistic that is calculated as an approximation should be termed "the capacity for increase (r_c) while the more complicated and accurate statistic should be termed "the innate capacity for increase in numbers (r_m)". The equation for calculating r_c is

$$r_c = \frac{\log e\ R_o}{T_c} \qquad (4)$$

According to Andrewartha & Birch (1954) r_m is a statistic that gives a summary of those physiological characteristics of an animal that are related to its ability to multiply. These characteristics are inherent to the animal and therefore make r_m as characteristic of the animal as any morphological characteristic. Although r_m is characteristic for each species Smith (1954) indicates that it might consist of either negative or positive values, as this value is influenced by environmental conditions. Thus a r_m value of 0 indicates the ecological equilibrium of a population while a high r_m value and short generation time is associated with smaller individuals. In this respect the value of r_m can be regarded as an index of the harshness of the environment. A very high maximum value of r_m might be of value to an organism which must reproduce itself rapidly while environmental conditions are suitable. A high value under other conditions might be a selective disadvantage.

According to Shiff & Husting (1966) it seems that the usefulness of r_m is not in the specific highest values obtained for a species, but in the range of values obtained under specified experimental conditions. If r_m does not vary much over a wide range for a specific environmental factor, it is reasonable to expect that factor to be relatively unimportant in controlling the rate of increase of the species concerned.

According to Birch (1948) the intrinsic rate of increase is determined to a much greater extent by the rate of oviposition in the first couple of weeks of adult life than by the total number of eggs laid in the life span of the adult, even although only 27% of the total number of eggs are laid in the first two weeks. With each successive week eggs laid make a progressively smaller contribution to the value of r_m. In the case of *Calandra (Sitophilus) oryzae* (L.) the value of r_m is 56% accounted for by the first week of adult life. The first two weeks combined contributed 85% and the first three weeks combined totalled 94%. The 14th week contributed only 0,02%.

The importance of the first few weeks of egg production has also been demonstrated by De Kock (1973) with *B. pfeifferi* where r_m was 99,8% accounted for by the first six weeks of egg production. The number of eggs produced at this stage represented only 29,5% of the total number of eggs laid during the life span of the adults. Similar conclusions were reached by DeWitt (1954b) when calculating r_m for *P. gyrina*.

Of corresponding importance is the accurate determination of the pivotal age for the first age category in which eggs are laid. In the case of *C. (S.) oryzae* (Birch, 1948) an error of half a week caused an error of 8% in the estimation of r_m. In the case of *B. pfeifferi* (De Kock, 1973) an error of 18% in the calculation of r_m would have been committed if the first age category had been miscalculated by half a period. Cole (1954) points out the fact that the age at which reproduction begins is one of the most significant characteristics of a species.

2.2.6 The net reproduction rate (R_o)

This is the rate of multiplication in one generation (Lotka, 1945) and is best expressed as the ratio of total female births in two successive generations. This is called R_o and is determined from age specific fecundity and survival rates and is defined as

$$R_o = \int_0^\infty l_x m_x d_x \qquad (5)$$

The product of $l_x m_x$ is obtained for each age group and the sum of these products $\Sigma l_x m_x$ is the value R_o. It is important to note the statement of Birch (1948) that the comparison of two or more populations by means of R_o may be quite misleading unless the mean lenghts of the generation are the same. For this reason the parameter R_o has limited value and it must always be considered in relation to the length of the generation.

2.2.7 Generation time (T_c)

The average age of the mothers of newborn offspring produced by a cohort is defined by Collier *et al*. (1973) as one generation, T_c and is given by the equation

$$T_c = \frac{\int_0^\infty x l_x m_x d_x}{\int_0^\infty l_x m_x d_x} \qquad (6)$$

T_c thus defined is the mean of the $l_x m_x$ distribution. In reality the females in a cohort produce offspring at various ages as described by the m_x distribution. If, instead all the offspring were produced by the cohort when mothers were of age T, the nett effect would be that the population would grow at the same rate as before. The numerical value of T_c as defined above is usually calculated by the approximation

$$T_c = \frac{\Sigma x l_x m_x}{\Sigma l_x m_x} \qquad (7)$$

This definition of Collier et al. (1973) is virtually identical to that of Laughlin (1965).

2.2.7 The finite rate of increase (λ)

The finite rate of increase (designated λ by Andrewartha & Birch, 1954) is the anti-log of r_m and indicates the number of times a population will multiply per time unit (Birch, 1948).

DeWitt (1954b), Shiff (1964a), Prinsloo (1966) and Sturrock (1966) calculated r_m according to equation 2. Shiff & Husting (1966), Combrinck (1968) and Williams (1970b) used equation 4 to calculate r_c while Harrison et al. (1970) and Sturrock & Sturrock (1972) do not state the equation used in their work. Jennings et al. (1973) and De Kock (1973) used equation 3 to calculate r_m and this equation was also used during this investigation.

According to Birch (1948) the calculation of r_m using equation 4 (Laughlin's r_c) leads to an underestimation of r (=r_m) owing to the approximation of T. Laughlin (1965) confirms that r_m is greater than r_c except when population numbers are stationary (R_o= 1) and he indicates that the relation between r_m and r_c is not linear at high values of n (reproductive period) and/or R_o. De Kock (1973) analysed a life table of *B. pfeifferi* to study this phenomenon. With a R_o value of 16,9556, r_c approaches r_m quite closely, but as the value of R_o increases r_c progressively decreases while r_m increases to stabilize on the fifth V_x entry in the life table. He concludes that the use of r_m has obvious advantages over the use of r_c. Although r_c was calculated for comparative purposes during this investigation, all discussions are based on the value of r_m. For the compilation of life tables fortnightly intervals were used. The number of surviving snails at the start of a forthnight was noted and the total number of fertile eggs produced during that fortnight was used in the calculations. This was done because the species under investigation were all self fertilizing hemaphrodites and consequently all progeny have to be taken into account.

When compiling life tables of freshwater snails it is essential that the exact number of eggs produced by the snails during the experiments should be established. In experiments, such as the present one, where up to sixteen cohorts were kept simultaneously, the counting of all the eggs becomes impossible due to the time consumed by the performance of this task. To alleviate this situation De Kock (1973) developed a procedure with which it is possible to calculate accurately within predetermined limits the total egg production of the snails, but which only involves the actual counting of a fraction of this total.

In broad outline the development of this procedure embraced the following steps: an accurate count of the number of egg clutches as well as the number of eggs produced every day by a cohort of *B. pfeifferi* was kept for 18 weeks. With the aid of this data it was possible to establish the exact egg production of the cohort for periods of seven days by adding the daily totals for seven days. The means and standard deviations of the num= number of eggs per clutch, clutches per snail and consequently also eggs per snail for each of the 18 weekly periods were determined. With the aid of these details, an equation was developed with which the fraction of the accumulated egg clutches that need to be counted, could be calculated. The existence and usefulness of such an equation is subject to its accuracy. In this respect the difference between the estimated egg production using De Kock's (1973) equation and the actual or true egg production was equal to or less than 5%, 95% of the times it was used. The regression between the accumulated clutches and the percentage proportion in which the eggs have to be counted is closely described ($100R^2$= 98%) by a power curve: ln(proportion)= 7,9846-0,7630 ln (accumulated masses). From this curve it is possible to establish directly the fraction of accumulated egg clutches which have to be counted. By determining the mean number of eggs per clutch in this fraction of the total accumulated during the seven day period and then multiplying the mean by the total number of egg clutches produced during this interval an estimate of the total number of eggs produced can be obtained. The larger the number of egg clutches accumulated becomes the smaller the percentage of this total that has to be counted, becomes.

As the calculation of the fraction of egg clutches to be counted are based on the means and standard deviations of eggs produced by *B. pfeifferi* the use of this equation as supplied by De Kock (1973) is restricted to those species such as *B.(B.) tropicus* and *B. (Physopsis)* spp. that have more or less the same values for these statistics. As such, this technique was therefore employed for the calculation of the egg production of these three species. The average number of eggs per egg clutch and the number of egg clutches produced during a given period by *L. natalensis* are respectively much higher and lower than that of *B. pfeifferi*. As a result of this the equation developed by De Kock (1973) could not be used for this particular species. To adapt De Kock's (1973) proportional egg counting technique for *L. natalensis*, eggs of this species were accumulated for sixteen consecutive weeks. Following the method described by the latter author the mean number of eggs per clutch as well as the standard deviations were calculated. With the aid of this data the regression between the accumulated clutches and the percentage proportion of egg clutches that have to be counted is fairly closely described ($100R^2=96\%$) by the power curve $y=71{,}8960e^{-0{,}0006x}$. By means of this regression equation it is possible to calculate the proportion of egg clutches of which the eggs have to be counted (figure 2).

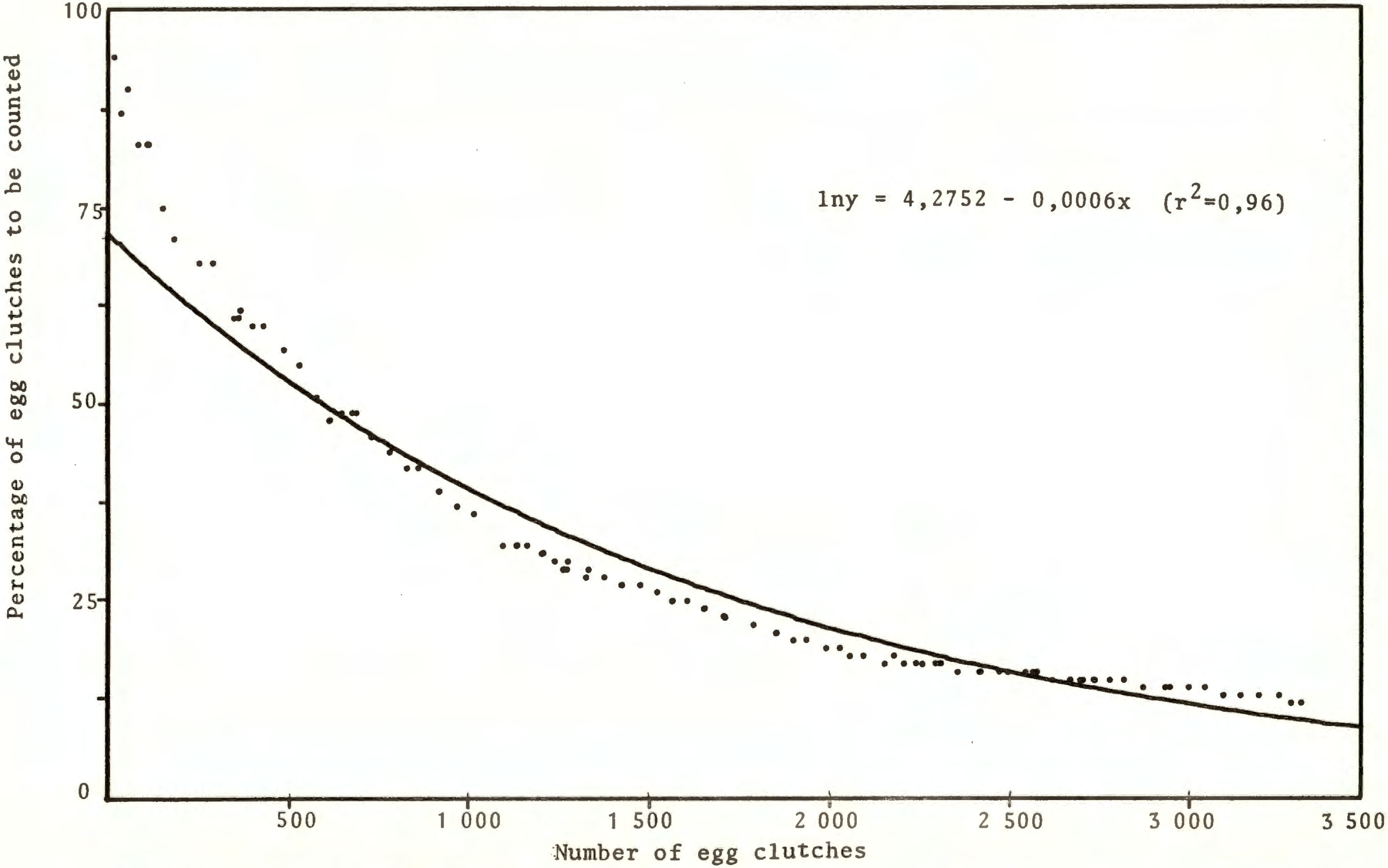


Figure 2. Calculation of the fraction of accumulated egg clutches of *L. natalensis* that have to be counted

3. RESULTS AND OBSERVATIONS

3.1 Observations

Ackerman (1972) as well as De Kock (1973) reported frequent copulations in their cohorts of *B.(B.) tropicus* but both these authors failed to see *L. natalensis* copulating. De Kock (1973) also failed to find any sign of copulation in the cohorts of *B. pfeifferi*, *B.(P.) globosus* and *B.(P.) africanus* which he experimented with. During the present investigation both *B.(B.) tropicus* and *B.(P.) globosus* were frequently seen to copulate while this was less frequently observed with *L. natalensis* and *B. pfeifferi*.

It is not clear what role copulation plays in the reproduction of these self fertilizing species. Isolated, non copulating *L. stagnalis apressa* kept by Noland & Carriker (1946) and *L. columella* kept by Winsor & Winsor (1935) produced more eggs than pairs or groups of these species and DeWitt (1954a) confirmed this for *P. gyrina* as well. These allegations are however contradicted by the findings of DeWitt (1967) who found pairs of *Physa pomilia* Conrad and *L. columella* to produce more eggs than isolated ones. This is further supported by Ritchie, Hernandey & Rosa-Amador (1966) who had similar experiences with *B. glabrata*. Pimentel (1957), however, could find no difference in the egg production of 100 isolated specimens of *B. glabrata* and that of 100 specimens that were kept in pairs. According to Bondesen (1950) and Duncan (1959) copulation is important due to it's fertilizing action and indirectly as a trigger mechanism that initiates egg production while DeWitt (1967) suggested that copulation resulted in greater egg production in *Helisoma duryi* Weatherby.

The phenomenon of snails leaving the water and adhering to the sides of the containers has been described for *B. glabrata* by Richards (1967) and for *B. pfeifferi* by Shiff & Garnett (1967) and Jennings et al. (1973). The latter authors ascribe it to an urge to reach more favourable conditions than those existing in the containers in which they are being kept. During the present investigation, however, hardly any snails indulged in this behaviour, not even at those conductivities which were decidedly unfavourable to them. The only exceptions were some specimens of *L. natalensis* and *B. pfeifferi* which did this at a time when mortality in their respective cohorts was high and reproduction had practically ceased.

Discussing the influence of light on the oviposition of snails De Kock (1973) concludes that strong daylight does not harm them. He nevertheless suggests that the aquaria should be protected from direct sunlight to prevent the establishment of algae which tend to block the supply pipes and which, according to Chernin & Michelson (1957a) and Wright (1960), influence the results. DeWitt & Sloan (1960) consider light unnecessary for the initiation of oviposition in *P. pomilia* and DeWitt (1967) even suggests that egg production in *P. pomilia* and *L. columella* might be inhibited by light. He concludes that the greater productivity of *P. pomilia* reared in the dark may be due to a tendency of some freshwater gastropods to lay their eggs during the night. This observation is supported by Cole (1925) who reports that *P. corneus* and *Planorbis trivolvis* Say oviposit exclusively at night. During the present experiment most of the eggs of all species were deposited during the night.

The frequent occurrence of mineral particles in the stomach region of various species of snails is well known. The importance of fine particles of grit in the gizzard has been demonstrated by Colton (1908) for *L. columella* and by Carriker (1946) for *L. stagnalis*. Calow (1970) and Storey (1970) have shown that the ingestion of mineral particles by *L. pereger* (Müller) results in more efficient trituration of food materials and influences growth. The importance of mineral particles in the diet of the species used during this investigation is not known and their gizzards could not contain any mineral particles anyway. The function of a grit filled gizzard is the efficient maceration of the more rigid food particles but since "Tetramin" is quite soft when wet, the presence of sand or grit particles is unnecessary.

The effect of low salinities on shell morphology

Crabb (1929) reported abnormal growth in *Lymnaea* bred in calcium free water and Schutte & Frank (1964) found the calcium content of waters to be correlated with population densities and shell fragility. Since such a large part of the snail (up to 90% dry mass in *Biomphalaria*) consists of calcium carbonate (Frank, 1963) any shortage of these particular ions could be expected to have serious repercussions for the snails.

The lowest conductivity at which *B.(B.) tropicus*, *B.(P.) globosus* and *B. pfeifferi* could be bred successfully was 180 µS. This water had a calcium content of 7 ppm (table 2) and must, according to Schutte & Frank (1964), be regarded as being very soft. These authors also found this water type to be unfavourable for all types of snails although it did not act as a limiting factor providing certain minimum quantities of ions were present in the water.

In the present experiment the shells of both *B.(B.) tropicus* and *B.(P.) globosus* exhibited varying degrees of abnormal growth and development as well as a high degree of fragility (plates 4 & 5). Apart from the fact that the shells were very fragile the following morphological features seemed to be affected. The aperture developed abnormally and many deviations from the average occurred. In both species the shapes of the columella and callus were abnormal and this quite often was the reason for the strange appearance of the aperture. In many specimens spiral development did not occur or was severely suppressed. Practically all the


4


5


6

snails suffered as regards growth rate and as adults, they were much smaller than most of the specimens of the same species at higher salinities.

The shells of *B. pfeifferi*, in contrast to those of the two species discussed above, exhibited no abnormalities as regards shape but after a while erosion of the umbilicus became apparent. (Plate 6.) In many cases this erosion was extremely serious often causing the complete disappearance of the umbilicus. The loss of such a large part of their shell, however, had no apparent effect on the snails which survived under these conditions for 12 fortnights.

The shells of *L. natalensis* were not visibly affected at this conductivity.

According to Deschiens (1956) a certain minimum concentration of calcium salts in the water is necessary for the snails to construct their shells which is formed by successive deposits of calcareous matter, conchiolin and mucus. Absence of lime (Ca^{2+}) leads to dystrophy of the shell and in particular the presence on the latter of whitish eroded patches caused by the corrosive action of humic or mineral acids.

3.2 Life tables of *B.(P.) globosus*

The life tables obtained at the different conductivities at which experiments were conducted are discussed first of all for each species separately and subsequently on the basis of a comparison of the different species experimented with.

180 μS

Survival was not very good since mortality started as early as the third fortnight and continued steadily for the following nine fortnights during which all snails died (table 3). The snails started producing eggs 48 days after hatching and main=

Table 3 : Life table of *B. (P.) globosus* at 180µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	0	18	0,9000	0	0
3,5	112	16	0,8000	7,0000	5,6000
4,5	591	14	0,7000	42,2143	29,5500
5,5	617	13	0,6500	47,4615	30,8500
6,5	1 707	11	0,5500	155,1818	85,3500
7,5	2 458	11	0,5500	223,4545	122,9000
8,5	1 855	11	0,5500	168,6364	92,7500
9,5	1 904	7	0,3500	272,0000	95,0000
10,5	1 126	5	0,2500	225,2000	56,3000
11,5	0	2	0,1000	0	0

$R_o = \Sigma V_x = 518{,}3000$

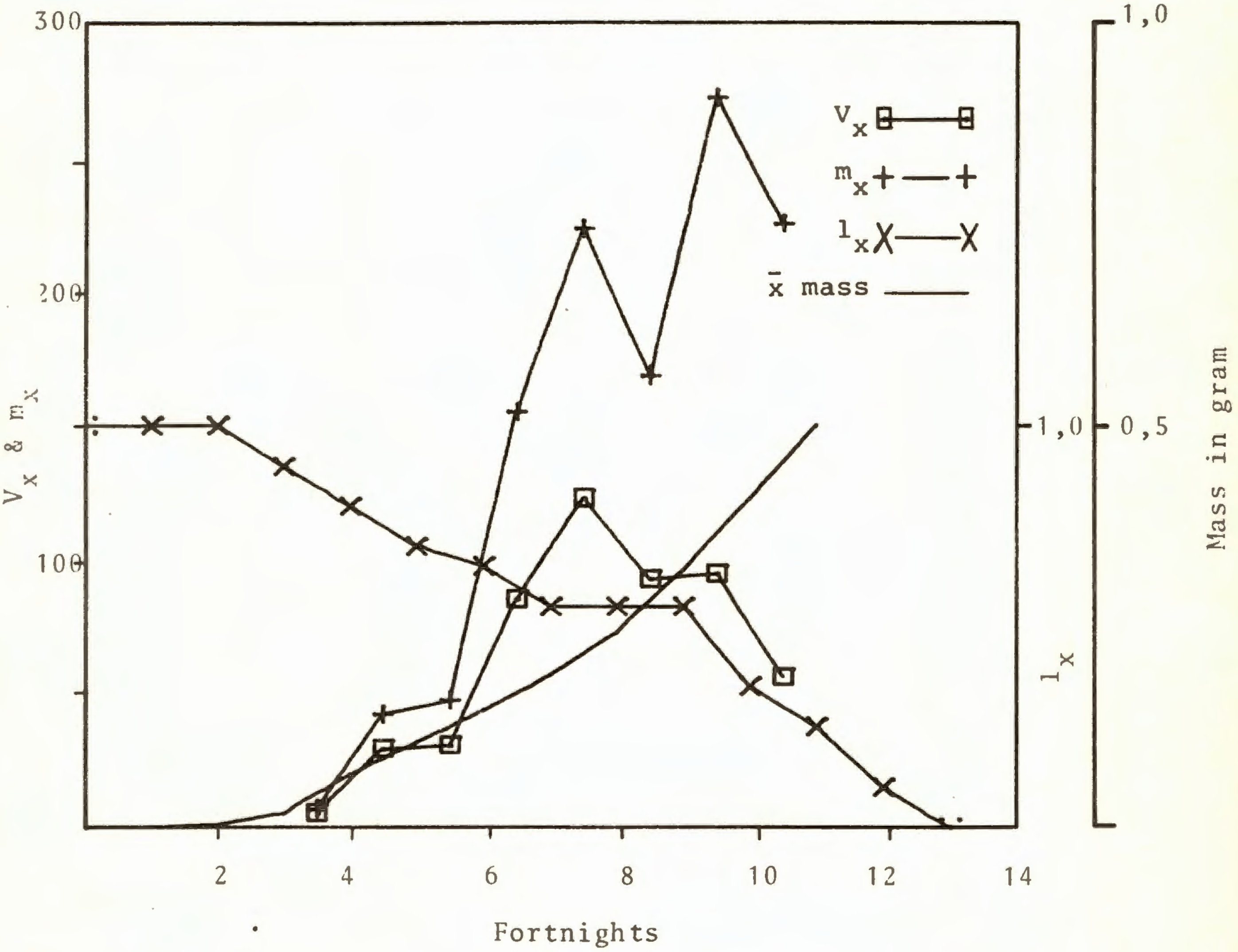


Figure 3. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 180 μS

tained this for eight fortnights. The natality curve (m_x) reached its highest peak during the tenth fortnight (figure 3). This was preceded by a serious slump during the ninth fortnight, caused by a drop in egg production,

250 µS

Survival was slightly better than at 180 µS with mortality starting after the third fortnight (table 4). These snails survived for only nine fortnights which is three less than the survival at 180 µS. Egg production commenced 43 days after hatching and continued for six fortnights. The natality curve (m_x) reached its peak during the sixth fortnigh (figure 4 and table 4). For this cohort higher values were recorded both for m_x and total egg production than for the cohort at 180 µS.

310 µS

Mortality started after the fourth fortnight (table 5 and figure 5) which is an improvement on both 250 µS and 180 µS and the cohort survived for 13 fortnights. Egg production started 28 days after hatching and lasted for 11 fortnights which is the longest reproductive period maintained by any cohort of *Physopsis* in this investigation. Likewise the interval between hatching and onset of egg production was the shortest recorded for this species. The natality curve reached its peak during the fifth fortnight (figure 5) one fortnight earlier than the cohort at 250 µS.

375 µS

For the first five fortnights this cohort exhibited an excellent rate of survival (table 6 and figure 6). After this, however, mass mortality occurred and all snails died during the sixth fortnight. Since there were no obvious changes in the physical and chemical environment the reason for the sudden mass mortali= ty is unknown. Egg production started 31 days after hatching.

Table 4 : Life table of *B. (P.) globosus* at 250µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	0	20	1,0000	0	0
3,5	1 213	19	0,9500	63,8421	60,6500
4,5	4 227	18	0,9000	234,8333	211,3500
5,5	5 119	18	0,9000	284,3889	255,9500
6,5	2 526	16	0,8000	157,8750	126,3000
7,5	744	7	0,3500	106,2857	37,2000
8,5	158	4	0,2000	39,5000	7,9000

$R_o = \Sigma V_x = 699{,}3500$

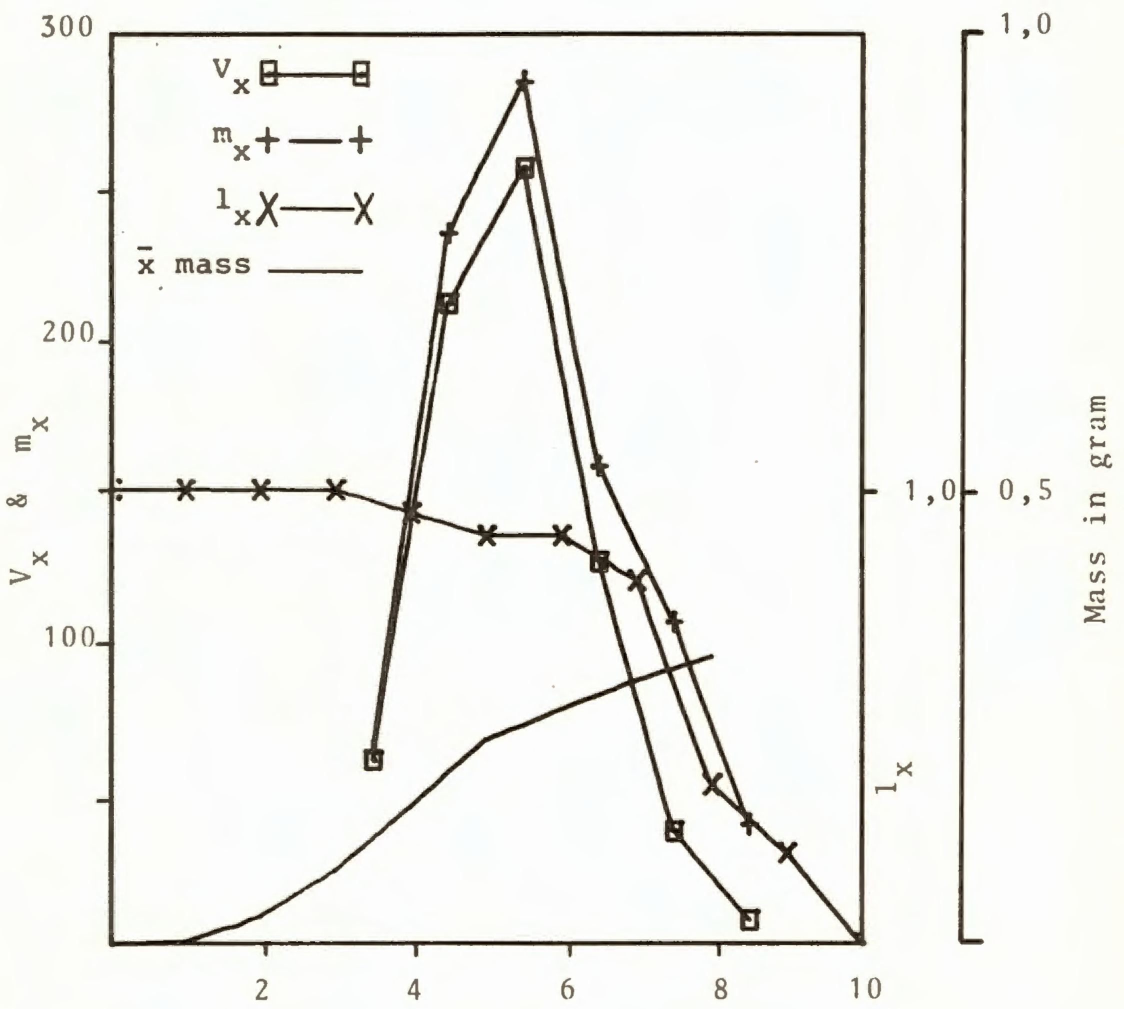


Figure 4. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 250 µS

Table 5 : Life table of *B. (P.) globosus* at 310μS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 520	20	1,0000	76,0000	76,0000
3,5	3 600	20	1,0000	180,0000	180,0000
4,5	6 078	19	0,9500	319,9474	303,9500
5,5	4 478	17	0,8500	263,4118	223,9000
6,5	4 400	16	0,8000	275,0000	220,0000
7,5	3 098	13	0,6500	238,3077	154,9000
8,5	2 403	13	0,6500	184,8462	120,1500
9,5	1 154	13	0,6500	88,7692	57,7000
10,5	367	10	0,5000	36,7000	18,3500
11,5	281	9	0,4500	31,2222	14,0500
12,5	71	6	0,3000	11,8333	3,5500

$V_o = \Sigma V_x = 1\ 372{,}5500$

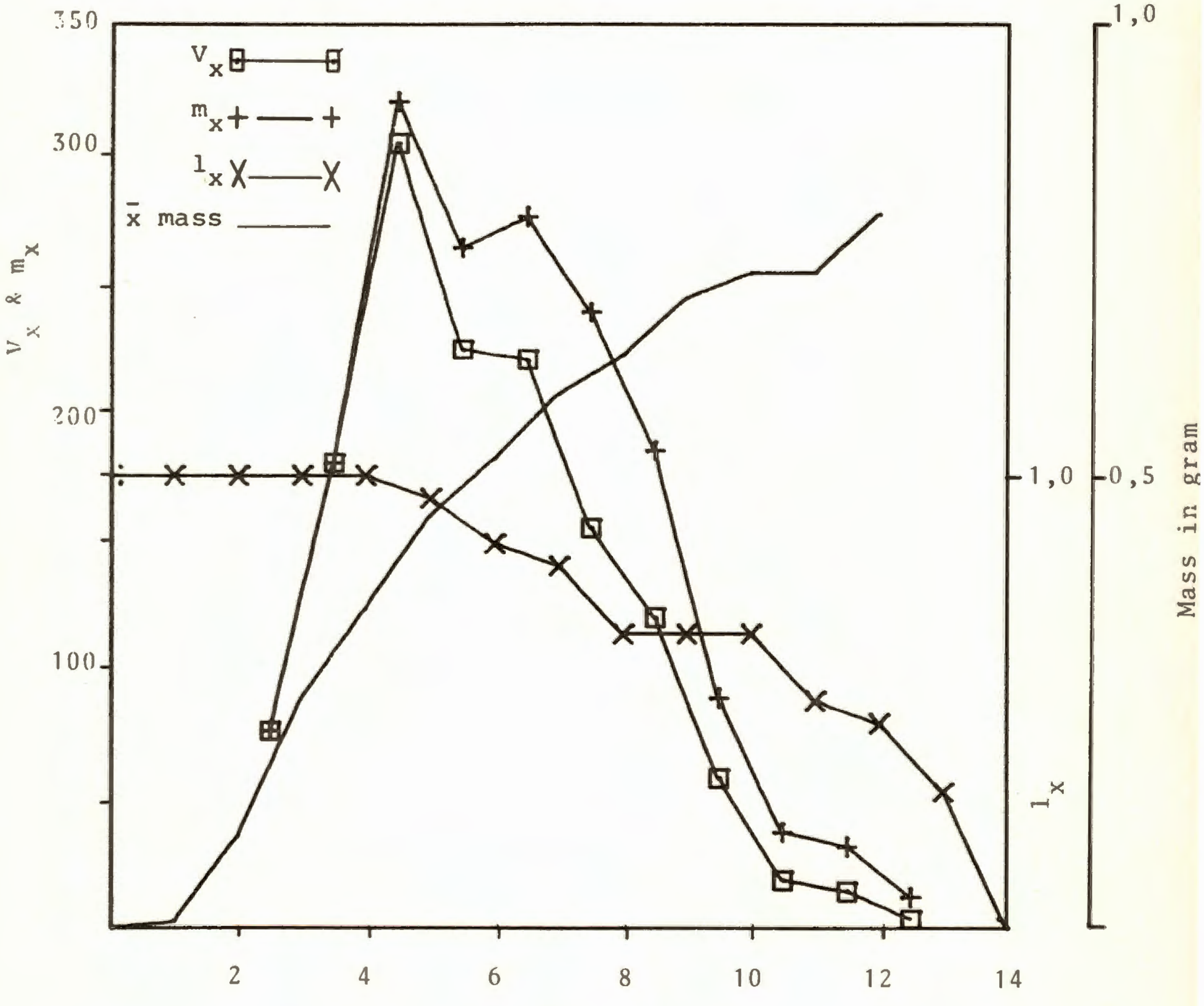
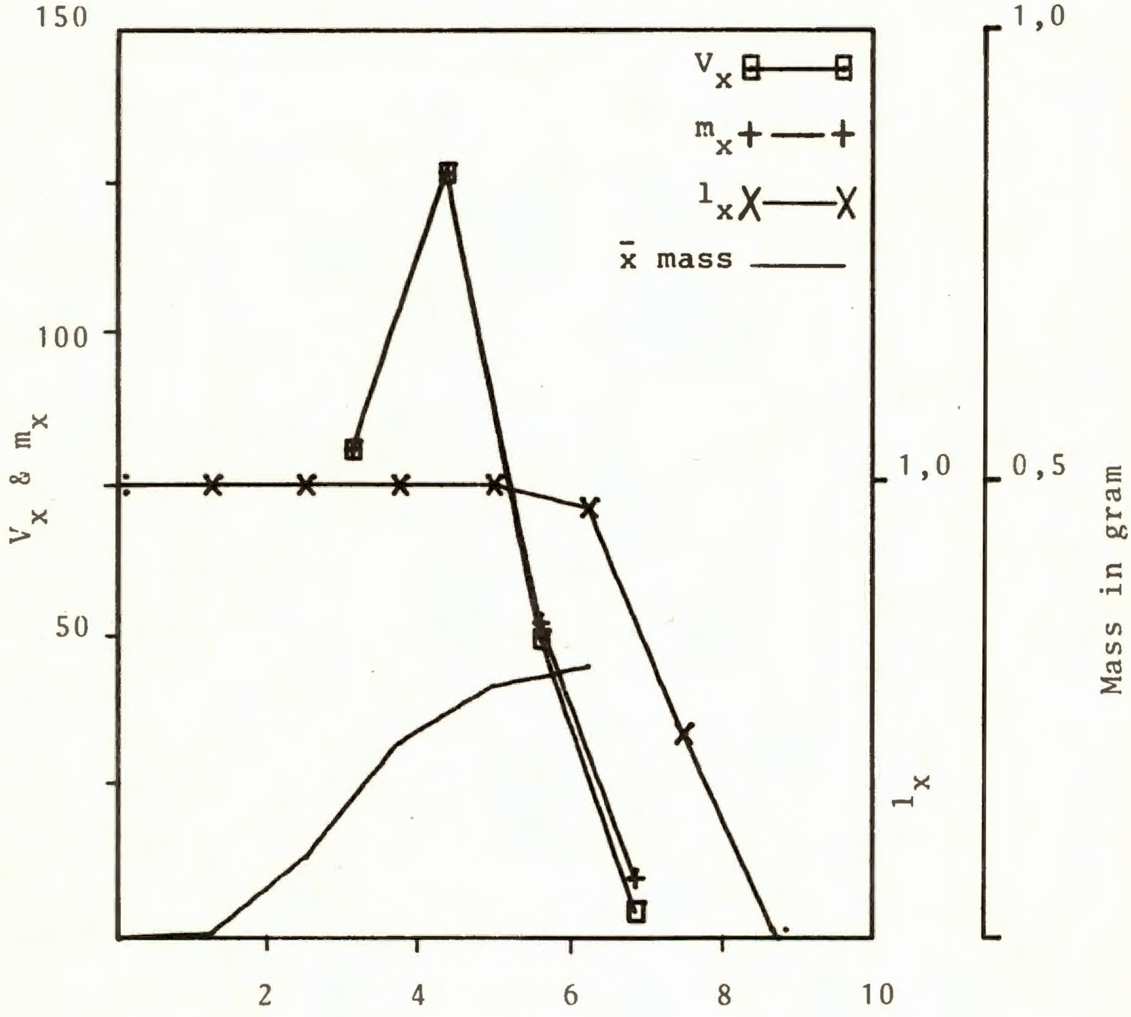


Figure 5. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 310 μS

Table 6 : Life table of *B. (P.) globosus* at 375µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 618	20	1,0000	80,9000	80,9000
3,5	2 532	20	1,0000	126,6000	126,6000
4,5	989	19	0,9500	52,0526	49,4500
5,5	89	9	0,4500	9,8889	4,4500

$R_o = \Sigma V_x = 261{,}4000$



Fortnights

Figure 6. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 375 µS

The first two fortnights of egg production compare favourably with those of the cohorts at 310 µS and 500 µS. After the second fortnight of egg production, however, the natality curve (m_x) declined sharply (figure 6). Only the first four fortnights of this cohort fit into the performance pattern of *B.(B.) globosus* obtained for the other six cohorts.

500 µS

Although mortality in this cohort started after the third fortnight it proceeded at a low rate and the cohort survived for 12 fortnights (table 7). Egg production commenced 37 days after hatching which is longer than that of the cohorts at 310 µS and 375 µS. This cohort had the highest mean egg production per interval per snail of all cohorts. The natality curve reached its peak during the sixth fortnight (figure 7) followed successively by a sharp drop and a slight recovery during the tenth fortnight. No eggs were produced during the last fortnight of survival.

625 µS

This cohort survived for ten fortnights with mortality starting after the third fortnight (table 8). Egg production started 37 days after hatching. It yielded the second highest mean egg production per snail per interval following closely behind the cohort at 500 µS. The highest egg production, reached during the third week of reproduction, was followed by a sharp drop (figure 8).

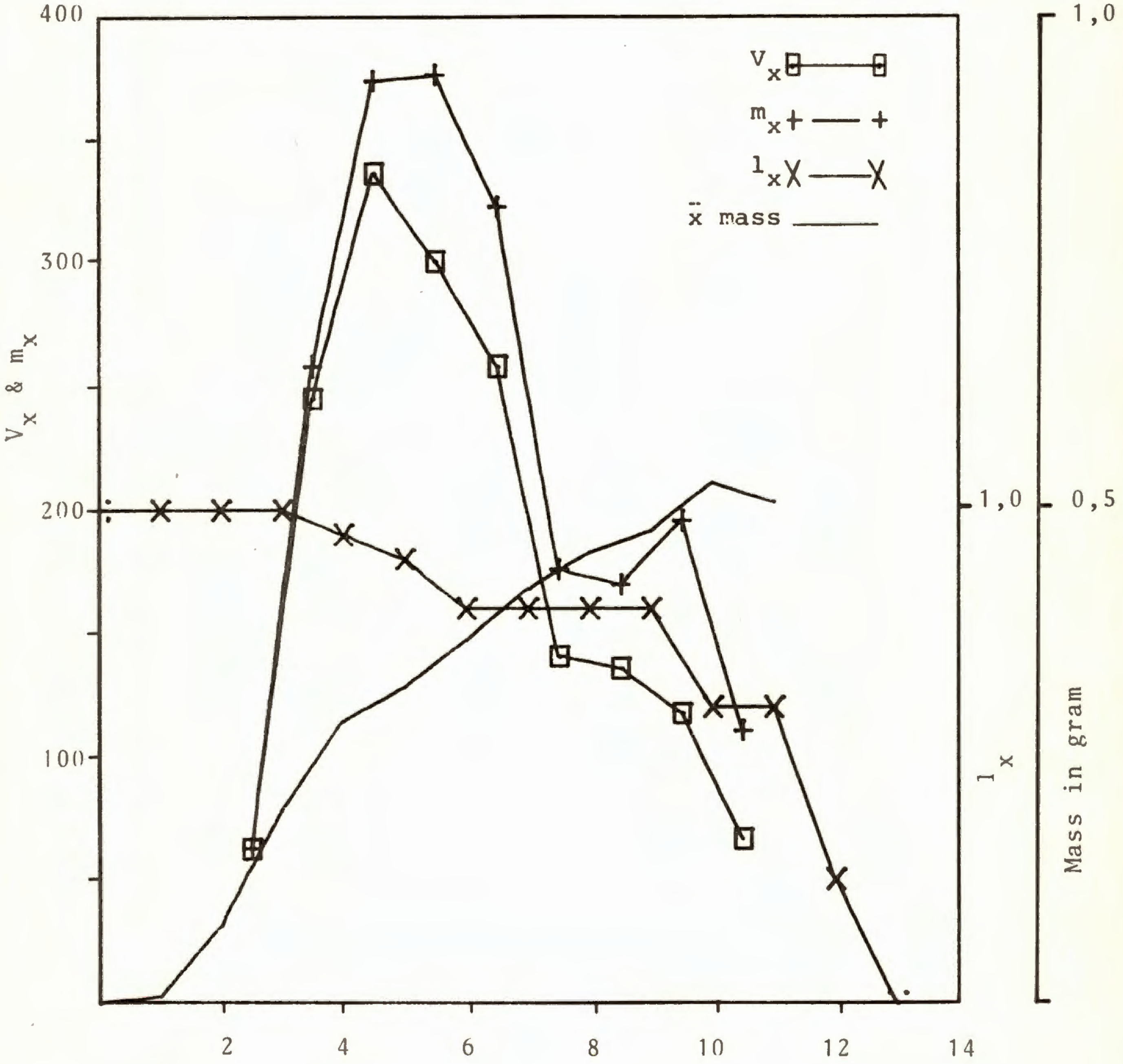
750 µS

Although mortality started immediately after the second fortnight (table 9) the rate at which snails died remained very low until the eighth fortnight. The cohort survived for 13 fortnights. Egg production started 37 days after hatching and during the last fortnight no eggs were produced. The natality curve

Table 7 : Life table of *B. (P.) globosus* at 500µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 249	20	1,0000	62,4500	62,4500
3,5	4 908	19	0,9500	258,3158	245,4000
4,5	6 731	18	0,9000	373,9444	336,5500
5,5	6 021	16	0,8000	376,3125	301,0500
6,5	5 167	16	0,8000	322,9375	258,3500
7,5	2 815	16	0,8000	175,9375	140,7500
8,5	2 716	16	0,8000	169,7500	135,8000
9,5	2 350	12	0,6000	195,8333	117,5000
10,5	1 325	12	0,6000	110,4167	66,2500
11,5	0	5	0,2500	0	0

$R_o = \Sigma V_x = 1\ 682,1000$



Fortnights

Figure 7. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 500 µS

Table 8 : Life table of *B. (P.) globosus* at 625µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	790	20	1,0000	39,5000	39,5000
3,5	4 682	19	0,9500	246,4211	234,1000
4,5	6 739	18	0,9000	374,3889	336,9500
5,5	3 988	18	0,9000	221,5556	199,4000
6,5	2 764	18	0,9000	153,5556	138,2000
7,5	1 096	16	0,8000	68,5000	54,8000
8,5	527	13	0,6500	40,5385	26,3500
9,5	304	8	0,4000	38,0000	15,2000

$R_o = \Sigma V_x = 1\ 061,5000$

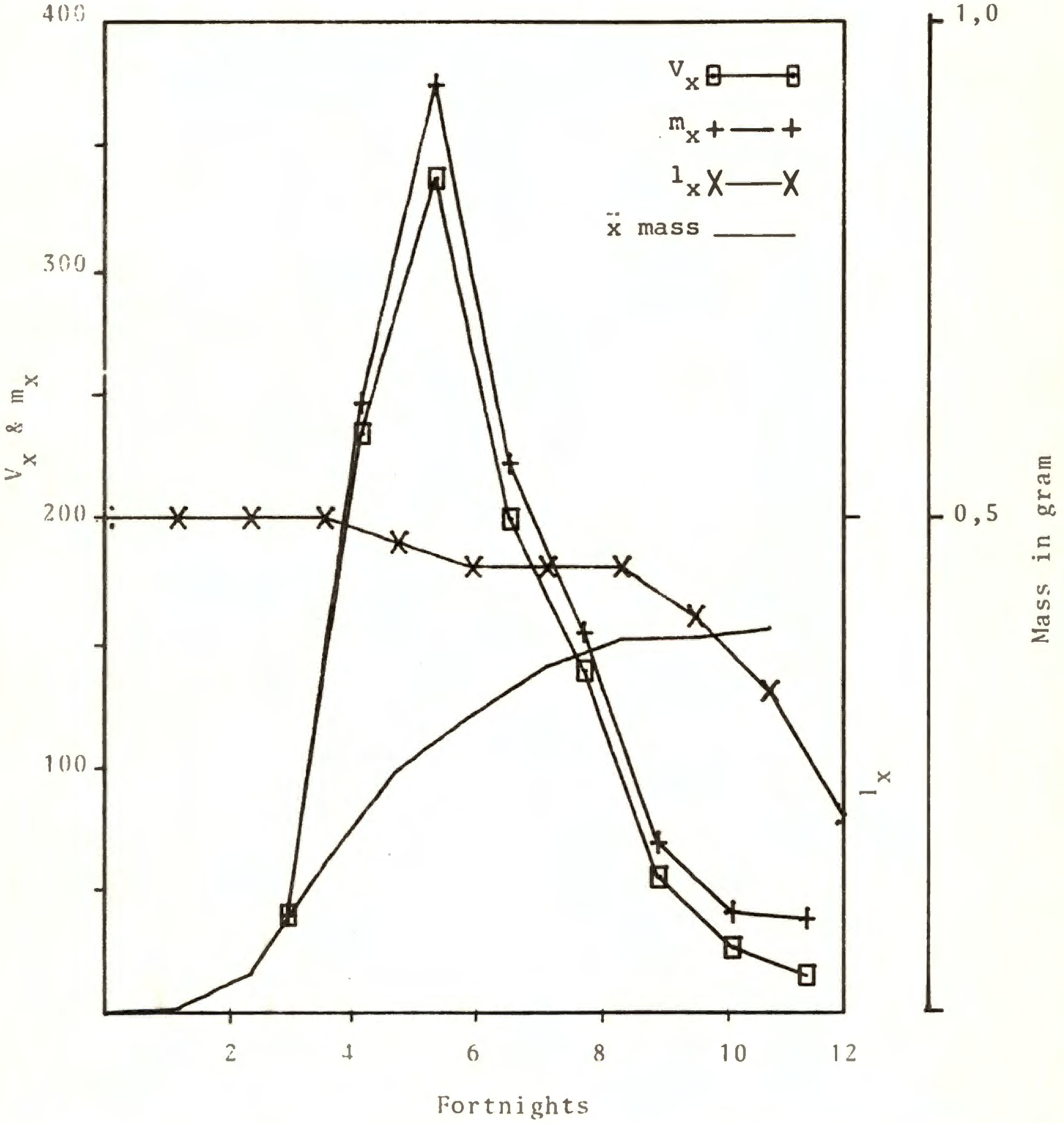


Figure 8. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 625 µS

Table 9 : Life table of *B. (P.) globosus* at 750µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	20	19	0,9500	1,0526	0,9743
3,5	622	19	0,9500	32,7368	31,1000
4,5	2 010	19	0,9500	105,7895	100,5000
5,5	3 769	19	0,9500	198,3684	188,4500
6,5	5 136	17	0,8500	302,1176	256,8000
7,5	3 909	17	0,8500	229,9412	195,4500
8,5	1 769	14	0,7000	126,3571	88,4500
9,5	2 022	11	0,5500	183,8182	101,1000
10,5	1 175	10	0,5000	117,5000	58,7500
11,5	281	7	0,3500	40,1429	14,0500
12,5	0	5	0,2500	0	0

$R_o = \Sigma V_x = 1\ 035,6243$

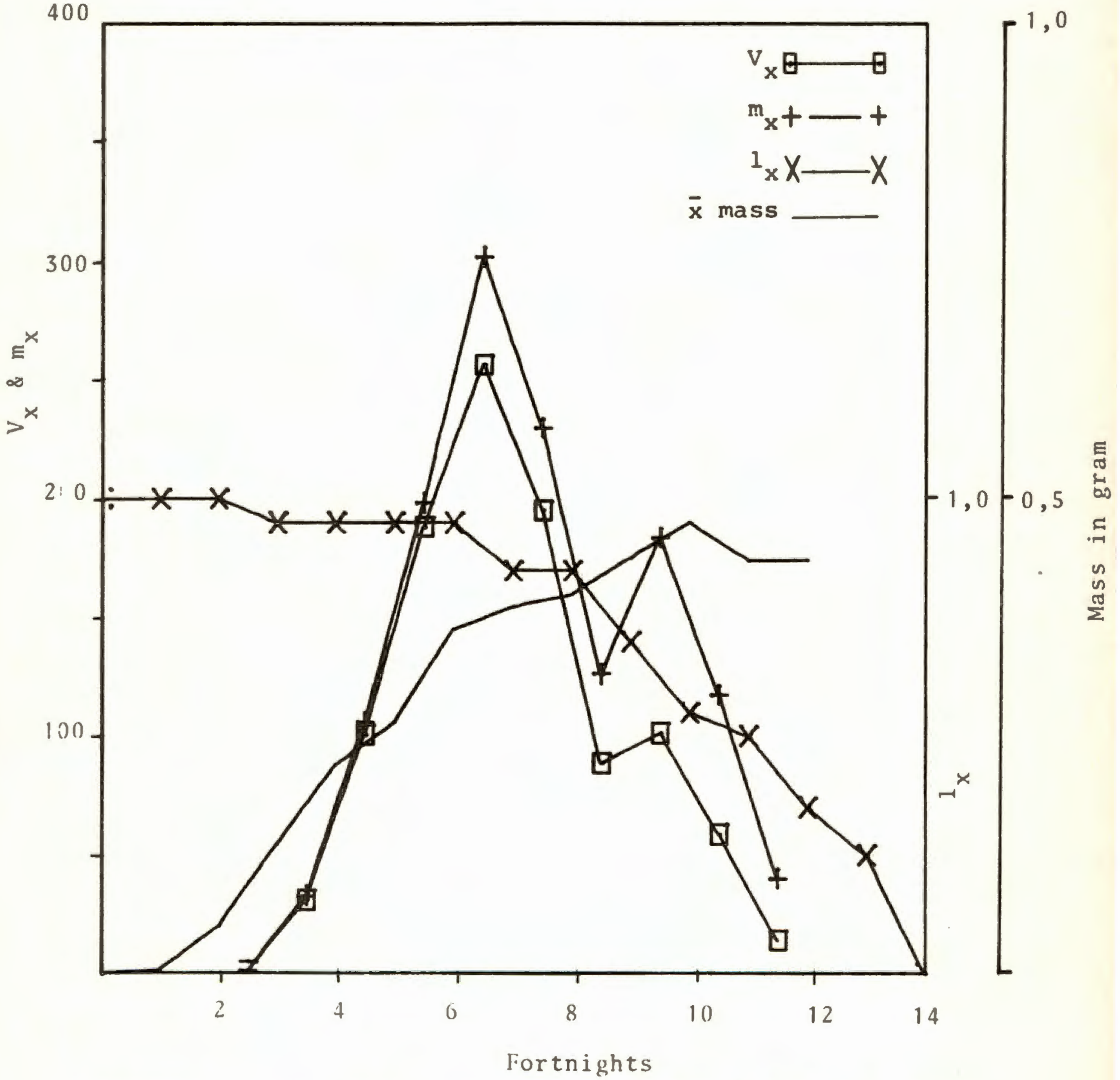


Figure 9. V_x , m_x , l_x values and mean fortnightly mass per snail of the cohort of *B.(P.)globosus* at a conductivity of 750 µS

reached its peak during the seventh fortnight, after which it dropped for two fortnights with a slight recovery during the tenth fortnight (figure 9).

Analysis

At all conductivities above 250 μS a high hatching percentage was obtained (table 10). A notable exception was the eggs at 310 μS of which only 44% hatched. As this low value does not fit into the overall pattern which emerged from the data in table 10, it has to be assumed that hatching at this conductivity was adversely affected by unknown factors. At the conductivities below 250 μS hatching percentages dropped to 67,96% and 58,33% at 180 μS and 125 μS respectively. At the latter conductivity the hatchlings did not survive for more than a couple of days. At 50 μS embryos developed very slowly and they all died after 14 days while still within the egg clutches.

There is no significant difference in the hatching time recorded for the eggs at the different conductivities (table 10). Apparently, therefore, this aspect was not influenced by the conductivities which these eggs had been subjected to. The interval between hatching and egg deposition was, however, decidedly influenced by conductivity. The cohort with the shortest interval was the one bred at 310 μS. Below this conductivity it increased with decreasing conductivities to a maximum of 48 days at 180 μS and above 310 μS it increased with increasing conductivities to 37 days at 750 μS. Although the hatching percentages were higher at the higher conductivities (625 μS and 750 μS) the interval between hatching and the onset of egg production was shortest at 310 μS and 375 μS.

Despite small differences in the rate of mass increase that are obvious from figure 10 the overall pattern of mass increase of the different cohorts is very similar. The best growth rate as well as the highest mean mass per specimen was recorded for the cohort at 310 μS. After an initial low rate of mass increa=

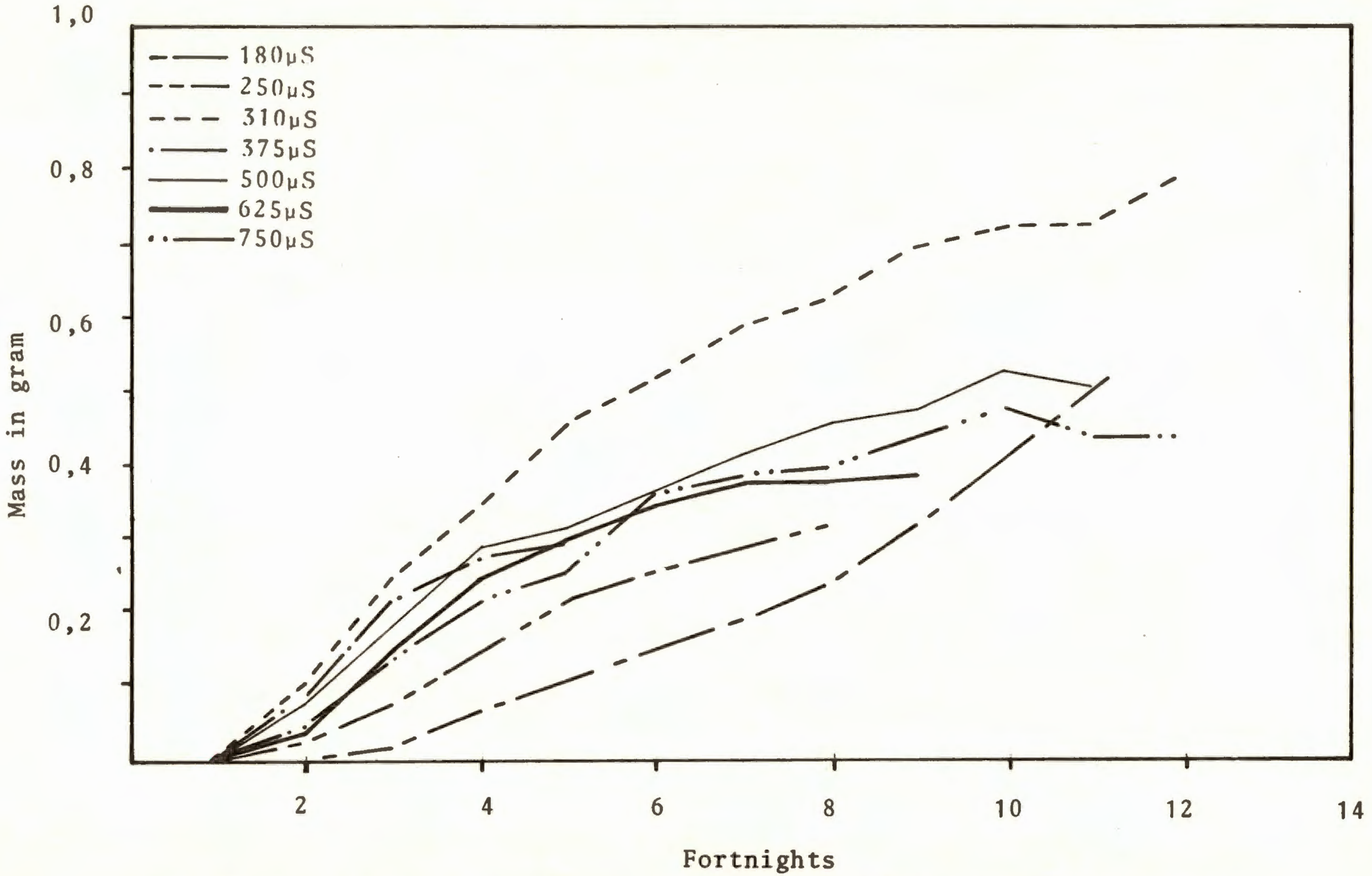


Figure 10. Mean fortnightly mass per snail of cohorts of *B.(P.) globosus* at the various constant conductivities based on the data contained in Appendix table 12

Table 10 : Population statistics of cohorts of *B.(P.)globosus*.

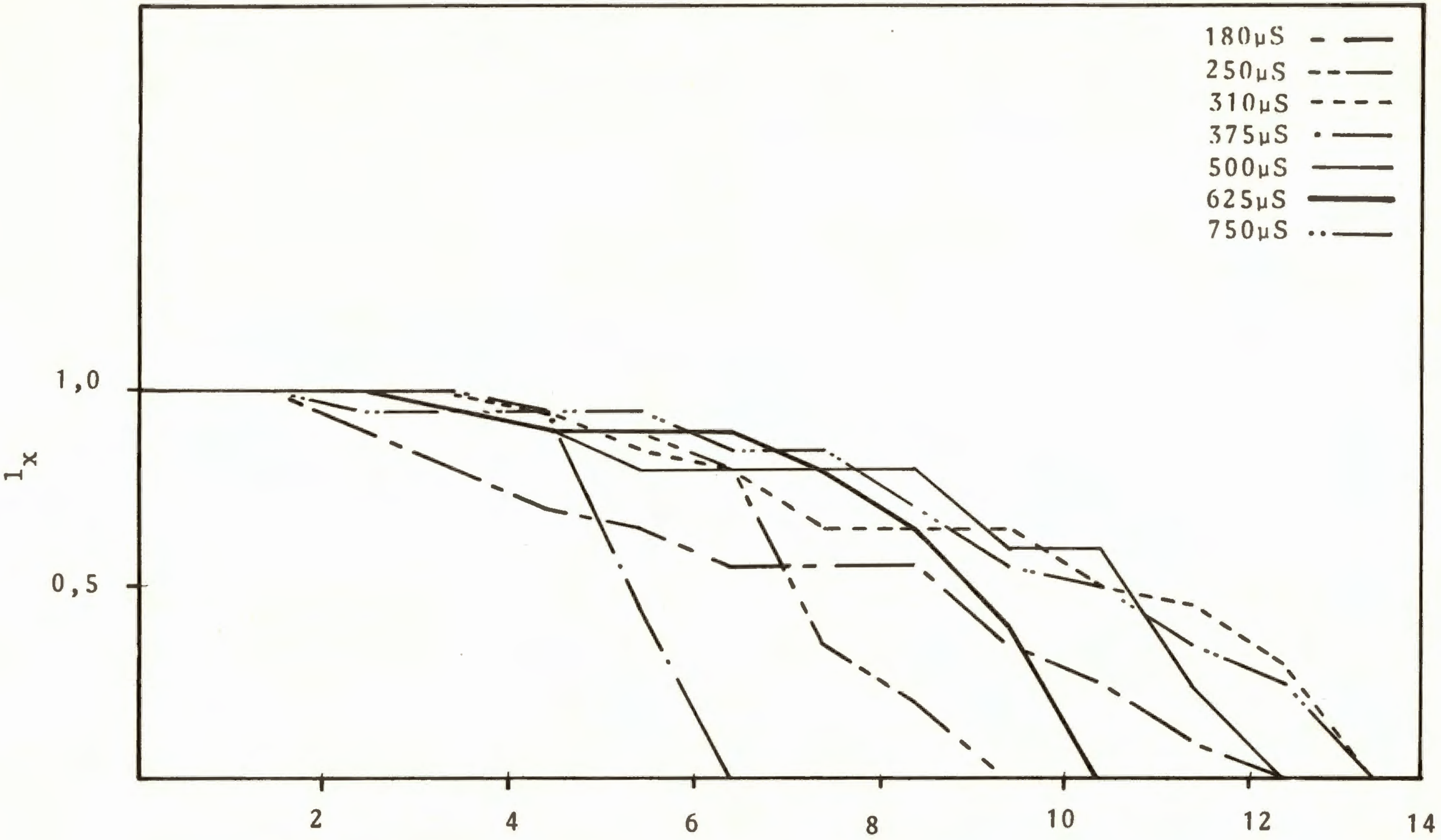
Conductivity	Hatching time*	Hatching percentage	Start of egg production*	λ	r_m	r_c	R_o	T_c
50µS	-	0	-	-	-	-	-	-
125µS	8	58,33	-	-	-	-	-	-
180µS	7	67,96	48	2,633	0,9679	0,794	518,30	7,873
250µS	8	82,18	43	4,027	1,3929	1,225	699,35	5,345
310µS	9	44	28	6,585	1,8848	1,243	1 372,55	5,813
375µS	8	84,76	31	6,361	1,8502	1,631	261,40	3,414
500µS	8	83,33	37	6,534	1,8770	1,238	1 682,10	6,000
625µS	8	95,49	37	6,016	1,7944	1,373	1 061,50	5,075
750µS	8	93,46	37	3,557	1,2689	0,995	1,035,62	6,977

*In days

r_m -range = 0,9169

se which continued for eight fortnights the cohort at 180 µS eventually attained a much higher rate of oncrease as well as the third highest mean mass per snail (appendix table 12). The latter can be attributed to the fact that this cohort survived for 11 fortnights compared to the eight fortnights of the cohort at 250 µS. Had the cohort at 180 µS survived longer it could possibly have improved on the performance of the snails at 310 µS because it showed the highest rate of increase during the last four intervals of its existence. There seems to be no relation between mass and onset of egg production. The cohort at 180 µS started depositing eggs when the mean mass per snail was only 0,0666 g while the cohort at 310 µS had a mean mass of 0,2520 g per snail when egg production started. Maturity is therefore not subject to any particular mass as long as a certain minimum age has been reached.

There were no significant differences between the survivorship (1_x) curves of the cohorts at 310 µS and 750 µS (figure 11). Both these cohorts survived for 13 fortnights which makes them the longest surviving cohorts of *B. (Physopsis)*. Although mortality set in early in both these groups it never approached the proportions reported for the cohort at 375 µS where mass mortalities occurred after the fifth fortnight (table 6). Up to this stage it appeared as if this cohort would at least equal or approach the performances of the cohorts at 310 µS and 250 µS. Although the cohort at 180 µS suffered a steady mortality rate throughout the experiment it nevertheless survived for 11 fortnights. In both the cohorts at 310 µS and 375 µS mortality only commenced after the fourth fortnight. Judging from figures 10 and 11 it seems as if both the growth rate and survival of at least the very young stages of *B.(P.) globosus* were adversely affected by low conductivities such as 180 µS. This assumption is supported by the low hatching percentage and the long period preceding egg production at 180 µS (table 10). It should be noted that with the exception of the cohort at 375 µS all the cohorts displayed remarkably prolonged periods of low mortalities rather than short periods of high mortalities.



Fortnights

Figure 11. The 1_x curves of the cohorts of *B.(P.)globosus* at the various constant conductivities

The reproductive rates (m_x) of the seven cohorts of *B.(P.) globosus* are compared in figure 12. Egg production set in during the third fortnight in all cohorts except the ones at 250 µS and 180 µS where it started one fortnight later. This delayed maturity could, therefore, be one of the effects of the lower conductivity ranges. The m_x values of the cohorts at 500 µS and 625 µS increased rapidly during the fourth and fifth fortnights and the highest m_x values were recorded for them. While the cohort at 500 µS was able to maintain its high reproductive rate, that of the cohort at 625 µS dropped sharply after reaching its peak during the fifth fortnight. These two cohorts were closely followed by the one at 310 µS which also reached its highest m_x value during the fifth fortnight and in addition to this kept up a relatively high reproductive rate after reaching its peak. The cohorts at 750 µS and 180 µS reached their highest m_x values much later han the other cohorts. In the latter case this occurred during the tenth fortnight, one fortnight before egg production ceased altogether. Although the cohort at 375 µS had the highest m_x value for the first fortnight of egg production (table 6) the mass mortality which occurred here prevented it from reaching a high m_x value. Judging from figure 12 it seems as if both high and low saline concentrations suppressed the reproductive rate of *B.(P.) globosus.*

A comparison of the data in appendix tables 13 and 14 and of the graphs in figures 13 and 14 with the m_x graphs in figure 12 reveals a remarkable resemblance between the graphs of the mean number of egg clutches per snail and the m_x curves of the corresponding cohorts. This implies that the mean number of egg clutches per snail contributed more towards the m_x values obtained than did the mean number of eggs per egg clutch. This, in turn, suggests that salinity affected the number of egg clutches produced by a snail more than it affected the numbers of eggs per egg clutch. Although the cohort at 310 µS produced the highest mean number of egg clutches per snail, both the cohorts at 500 µS and 625 µS yielded higher values for m_x. This was due to the fact that the cohort at 310 µS produced the egg

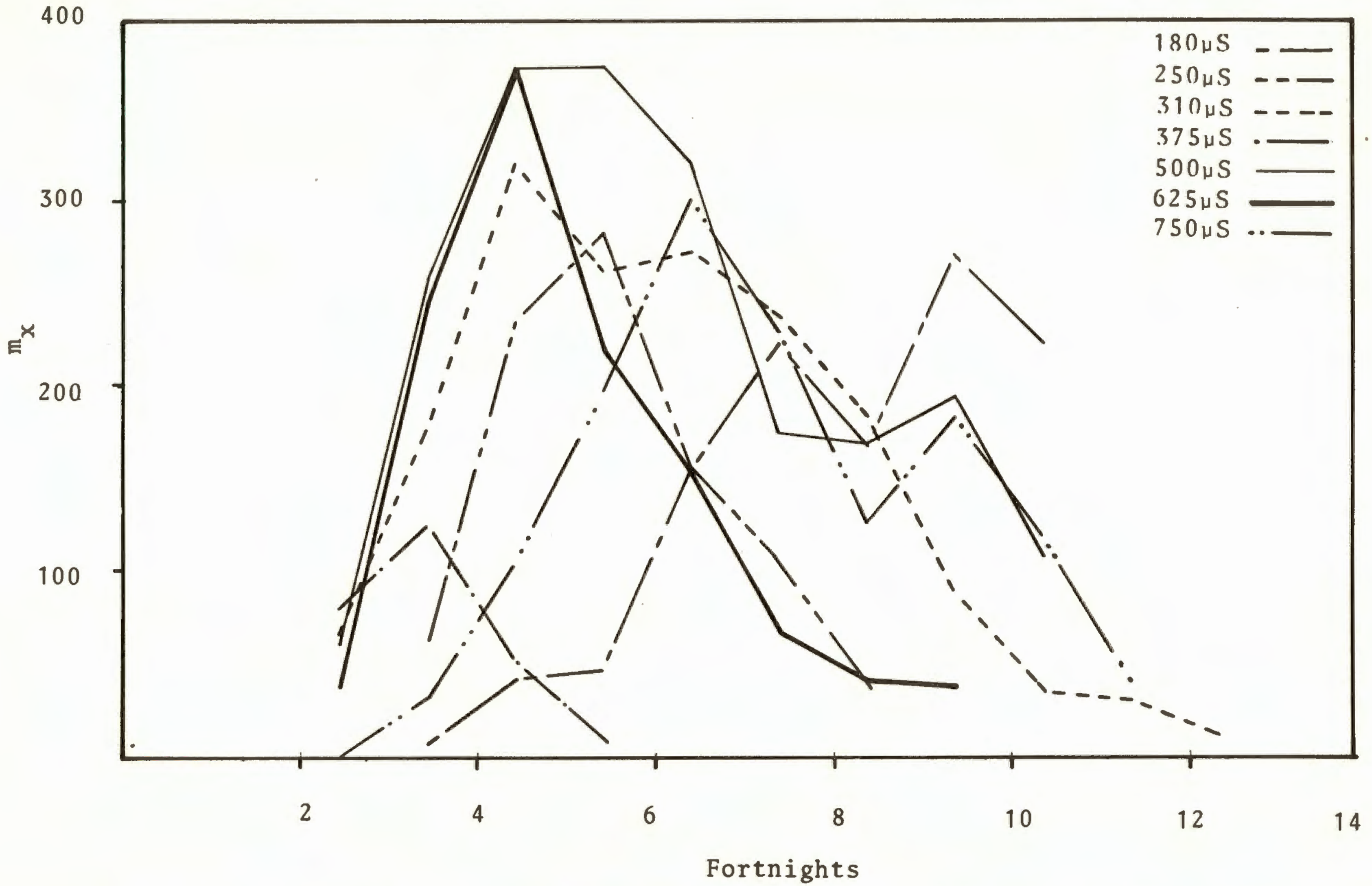


Figure 12. The m_x curves of the cohorts of *B.(P.)globosus* at the various constant conductivities

clutches with the lowest number of eggs (figure 14). The largest number of eggs per egg clutch was produced by the cohort at 250 µS. The cohort at 180 µS differed from the others in that the mean number of egg clutches per snail as well as the mean number of eggs per egg clutch, steadily increased throughout the experiment. This suggests that this cohort could not realize its full reproductive potential under the experimental conditions. In all the cohorts except the one at 180 µS the highest mean number of egg clutches per snail per fortnight was produced earlier than the highest mean number of eggs per egg clutch.

Only the cohort at 375 µS reached its highest m_x value before the onset of mortality. As a result of this it was the only cohort of *B.(P.) globosus* where the m_x and V_x curves hardly differ from each other (figures 6, 12 and 15). In terms of the highest values per fortnight the V_x sequence was 625 µS > 500 µS > 310 µS > 750 µS > 250 µS > 375 µS > 180 µS. When this is compared with the m_x sequence (500 µS > 625 µS > 310 µS > 750 µS > 250 µS > 180 µS > 375 µS) it can be seen that the better position in the V_x sequence of the cohorts at 625 µS and 375 µS must be linked with their higher survival rates. Although this appears paradoxical in the case of 375 µS where the snails survived for only five fortnights it must be borne in mind that this cohort suffered no mortalities during the first four fortnights (table 6). This also applies to the cohort at 310 µS (table 5).

The sums of the V_x values (R_o) of the different cohorts are presented in table 10 and the cumulative increase per fortnight in the value of R_o based on V_x values of the cohorts is graphically presented in figure 16. The R_o sequence was 500 µS > 310 µS > 625 µS > 750 µS > 250 µS > 180 µS > 375 µS. The cohort at 625 µS which yielded the highest V_x value per fortnight dropped back two places in respect of its R_o sequence because it did not maintain a high reproductive rate for the same length of time as the cohorts at 500 µS and 310 µS. For the same reason the cohort at 375 µS yielded a lower R_o value than the one at 180 µS and consequently also dropped back one place. It can be seen from the inclination of the graphs in figure 16 that

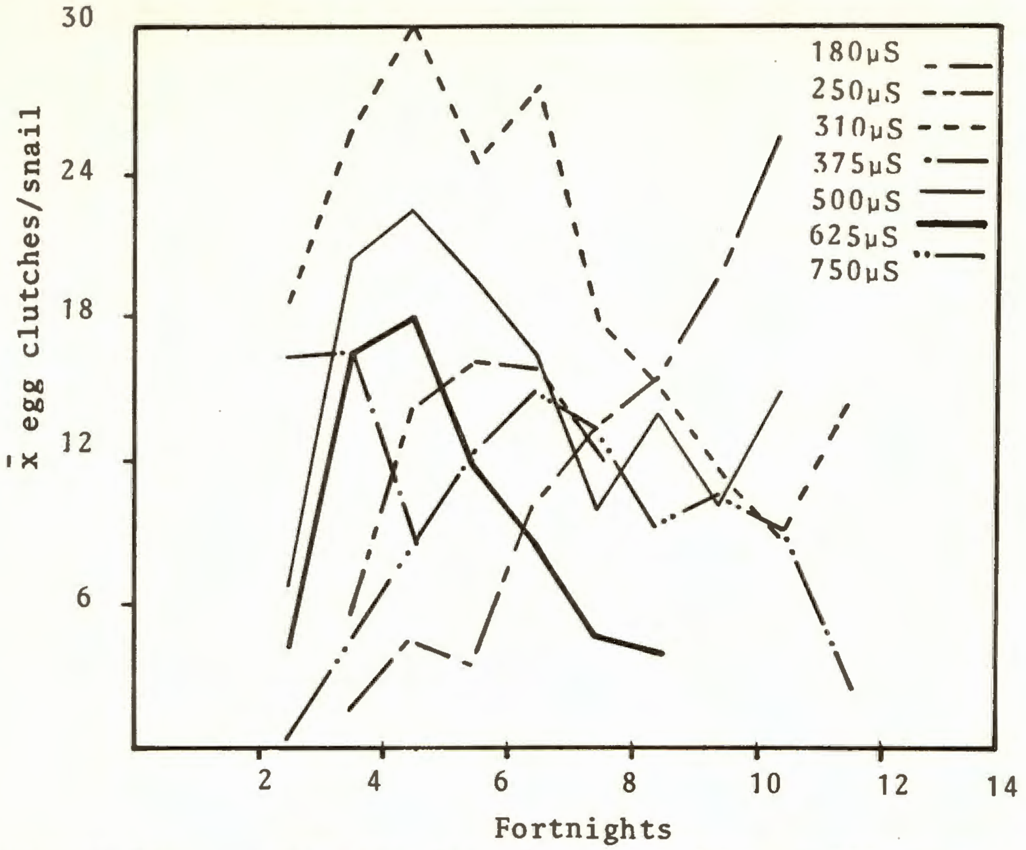


Figure 13. The mean fortnightly number of egg clutches per snail of *B.(P.)globosus* at the various constant conductivities based on the data contained in Appendix table 13

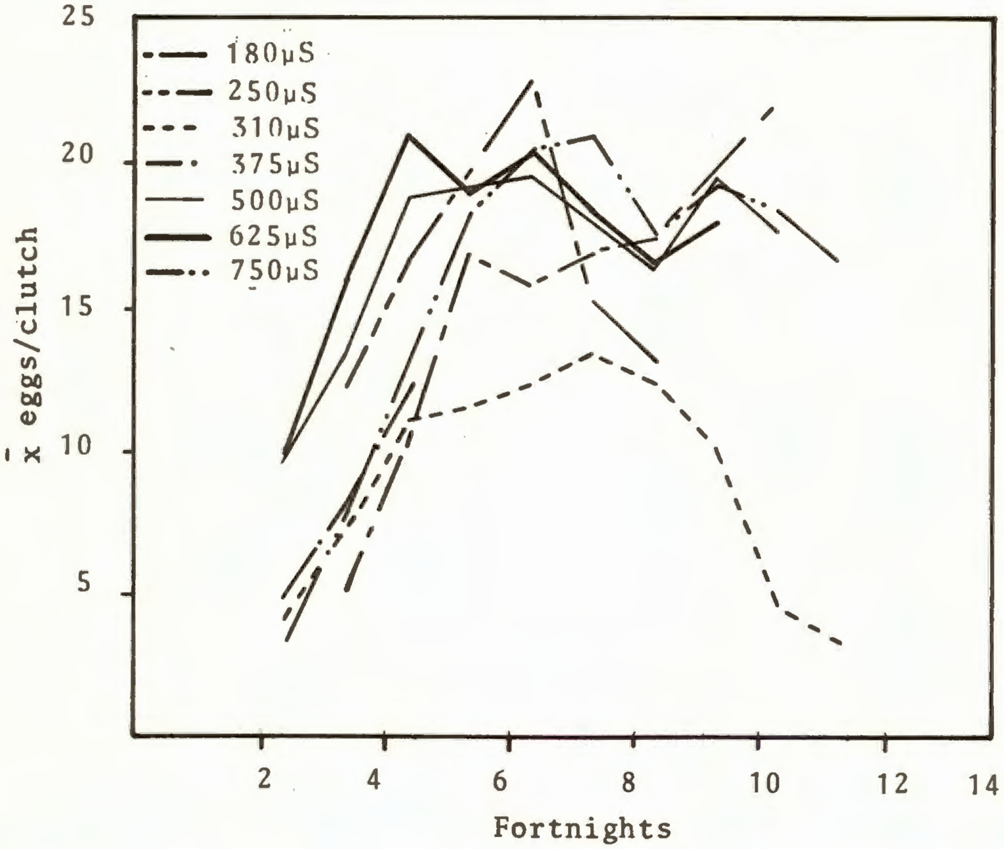


Figure 14. The mean fortnightly number of eggs per egg clutch of *B.(P.)globosus* at the various constant conductivities based on the data contained in Appendix table 14

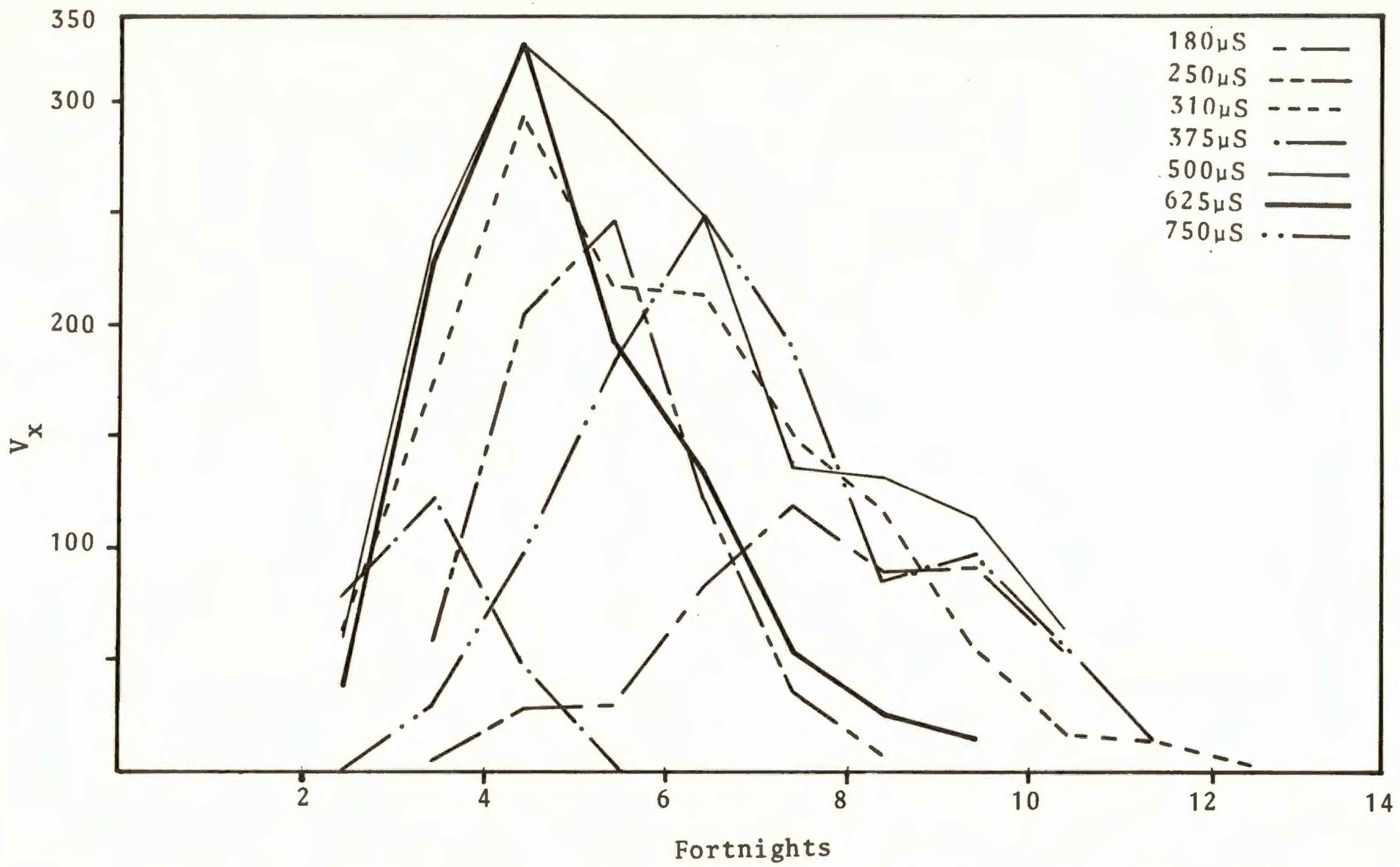


Figure 15. The V_x curves of the cohorts of *B.(P.)globosus* at the various constant conductivities

the cohort at 500 µS showed the highest rate of increase in the value of R_o per fortnight and that this cohort eventually also yielded the highest total R_o value. This performance was close=ly followed by that of the cohort at 310 µS.

From the definition of T_c it is clear that low T_c values are of great benefit to the successful survival of a species because little time is lost between birth and onset of reproduction. Generation time appears to have been affected by conductivity and the data in table 10 reveal that T_c definitely tended to increase at both the lower and the higher conductivity ranges. The low T_c value of the cohort at 375 µS should, however, not be compared with the T_c values of the other cohorts because the former reflects the unnaturally short reproductive period of the 375 µS cohort. The cohort with the highest R_o value did not, as might be expected, attain the lowest generation time and this complicates comparison of cohort performance.

From the foregoing it is evident that a success sequence based on any one of the respective statistics discussed above could be contradicted by a sequence based on any other statistic. Any final conclusions, therefore, have to be based on the results of the calculation of the intrinsic rate of natural increase (r_m) which incorporates all these statistics. Only this pro=vides an accurate picture of performance on which any compari=sons can be based.

The intrinsic rate of natural increase (r_m) and the finite rate of increase (λ) are presented in table 10. Although the cohort at 310 µS had the highest r_m value there is so little difference between this value and the r_m values of the cohorts at 375 µS and 500 µS that it would not be justifiable to dis=tinguish between them. The importance of the reproductive rate during the first couple of fortnights of reproduction is illustrated by the high r_m values of 1,8502 calculated for the cohort at 375 µS despite its short reproductive period. The

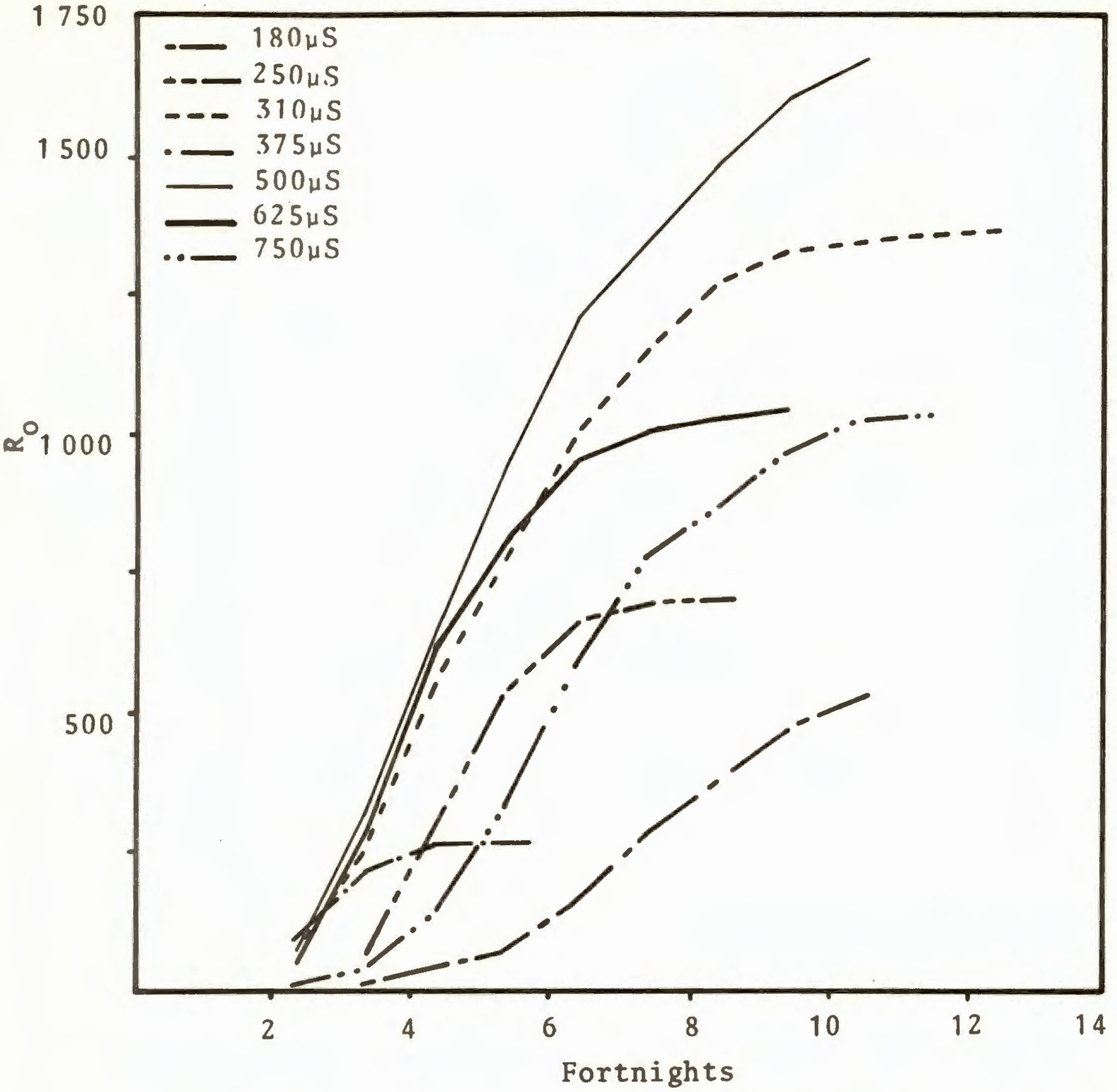


Figure 16. The increase in R_o value per fortnight of the cohorts of *B.(P.)globosus* at the various constant conductivities

importance of the first few weeks of reproduction on the calculation of r_m has also been demonstrated by Birch (1948), DeWitt (1954b) and De Kock (1973) and was discussed in detail under 2.2.1. During its first reproductive fortnight the cohort at 375 µS produced 1 618 eggs and this together with its low T_c value is the main reason for the high r_m value that was reached despite the low R_o value (table 10).

Since the r_m values of cohorts kept above 500 µS and below 310 µS tended to decrease, it may be assumed that the most favourable conductivity in which to breed *B.(P.) globosus* lies somewhere between 310 µS and 500 µS. Inspite of better T_c values, the cohorts at 250 µS and 625 µS did not reach such high r_m values as the other three cohorts mainly as a result of lower egg production during the first fortnights of egg production. The most important contributions to the differences in r_m values were undoubtedly made by m_x and T_c because up to the age where r_m can be influenced by survival, the l_x values for all cohorts remained reasonably similar. The positive r_m values calculated for all the conductivities tested reveal that *B.(P.) globosus* can survive and multiply at a conductivity range of between 180 µS and 750 µS. During this experiment a comparison of the finite rate of increase (λ) of the different cohorts confirms this conclusion because when $\lambda < 1$ a population is on the decline, when $\lambda \doteq 1$ a population remains static and when $\lambda > 1$ a population increases. In this case the lowest λ value was 2,633 (table 10).

3.3 Life tables of *B. pfeifferi*

180 µS

This cohort survived for 13 fortnights and during this time the mortality rate was very low (figure 17 and table 11). The survival pattern (l_x) was characteristic for *B. pfeifferi* and was similar to the l_x graphs obtained for this species by Jennings et al. (1973) and De Kock (1973). A comparison of the available

1_x curves on this species indicates that, with very few exceptions, this species exhibits a very high survival rate for practically the whole period of its existence with a very sudden increase in the mortality rate in the final stages. The cohort at 180 µS illustrates this survival pattern very well in that after 12 fortnights 80% of the snails were still alive and two fortnights later they had all died. Egg production started 26 days after hatching and continued throughout the lifetime of the snails. The fecundity (m_x) graph showed two peaks, one during the third fortnight and the second during the sixth fortnight. Due to the low mortality rate the V_x graph resembles the m_x graph quite closely.

250 µS

The typical *B. pfeifferi* survival pattern was again obvious and while slight mortalities did occur for four weeks (figure 18 and table 12) it was only after the eighth fortnight that mortalities reached significant proportions. Like the cohort at 180 µS the number of snails declined from 16 to 0 within two fortnights. Egg production started 20 days after hatching and a high reproductive rate was maintained. The highest fecundity (m_x) rate was reached during the fifth fortnight.

310 µS

For five consecutive fortnights no mortalities occurred (figure 19 and table 13) and although it started during the sixth fortnight when 19 snails were still alive, all the snails had died by the end of the seventh fortnight. A high reproductive rate was attained and was maintained for three consecutive fortnights so that instead of the m_x graph describing a peak it formed a plateau extending over a period of three fortnights. The m_x values were, however, considerably lower than those of the previous two cohorts. The snails only started producing eggs after 21 days which was later than in the case of the cohorts at 250 µS and 375 µS. Similarly the hatching time was two days

Table 11 : Life table of *B. pfeifferi* at 180µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	461	20	1,0000	23,0500	23,0500
2,5	4 938	20	1,0000	246,9000	246,9000
3,5	7 126	19	0,9500	375,0526	356,3000
4,5	6 167	19	0,9500	324,5789	308,3500
5,5	5 882	19	0,9500	309,5789	294,1000
6,5	7 514	19	0,9500	395,4737	375,7000
7,5	6 194	19	0,9500	326,0000	309,7000
8,5	6 601	18	0,9000	366,7222	330,0500
9,5	6 093	17	0,8500	358,4118	304,6500
10,5	5 771	16	0,8000	360,6875	288,5500
11,5	2 031	16	0,8000	126,9375	101,5500
12,5	559	5	0,2500	111,8000	27,9500

$R_o = \Sigma V_x = 2\ 966{,}8500$

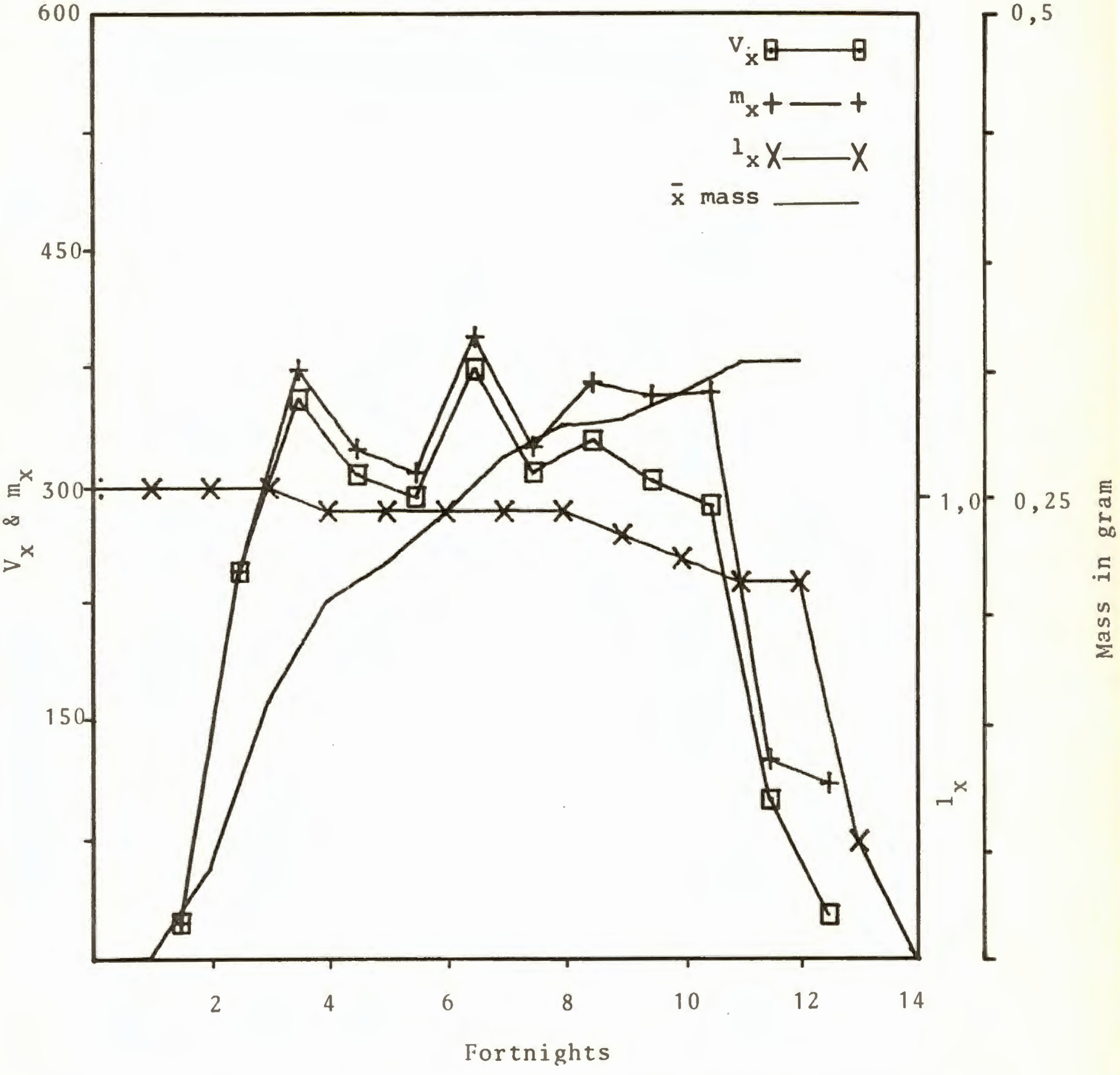


Figure 17. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.pfeifferi* at a conductivity of 180 µS

Table 12 : Life table of *B. pfeifferi* at 250µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	2 509	20	1,0000	125,4500	125,4500
2,5	7 515	20	1,0000	375,7500	375,7500
3,5	8 032	20	1,0000	401,6000	401,6000
4,5	9 451	19	0,9500	497,4211	472,5500
5,5	7 950	18	0,9000	441,6667	397,5000
6,5	6 667	18	0,9000	370,3889	333,3500
7,5	3 108	16	0,8000	194,2500	155,4000
8,5	167	4	0,2000	41,7500	8,3500

$R_o = \Sigma V_x = 2\ 269{,}9500$

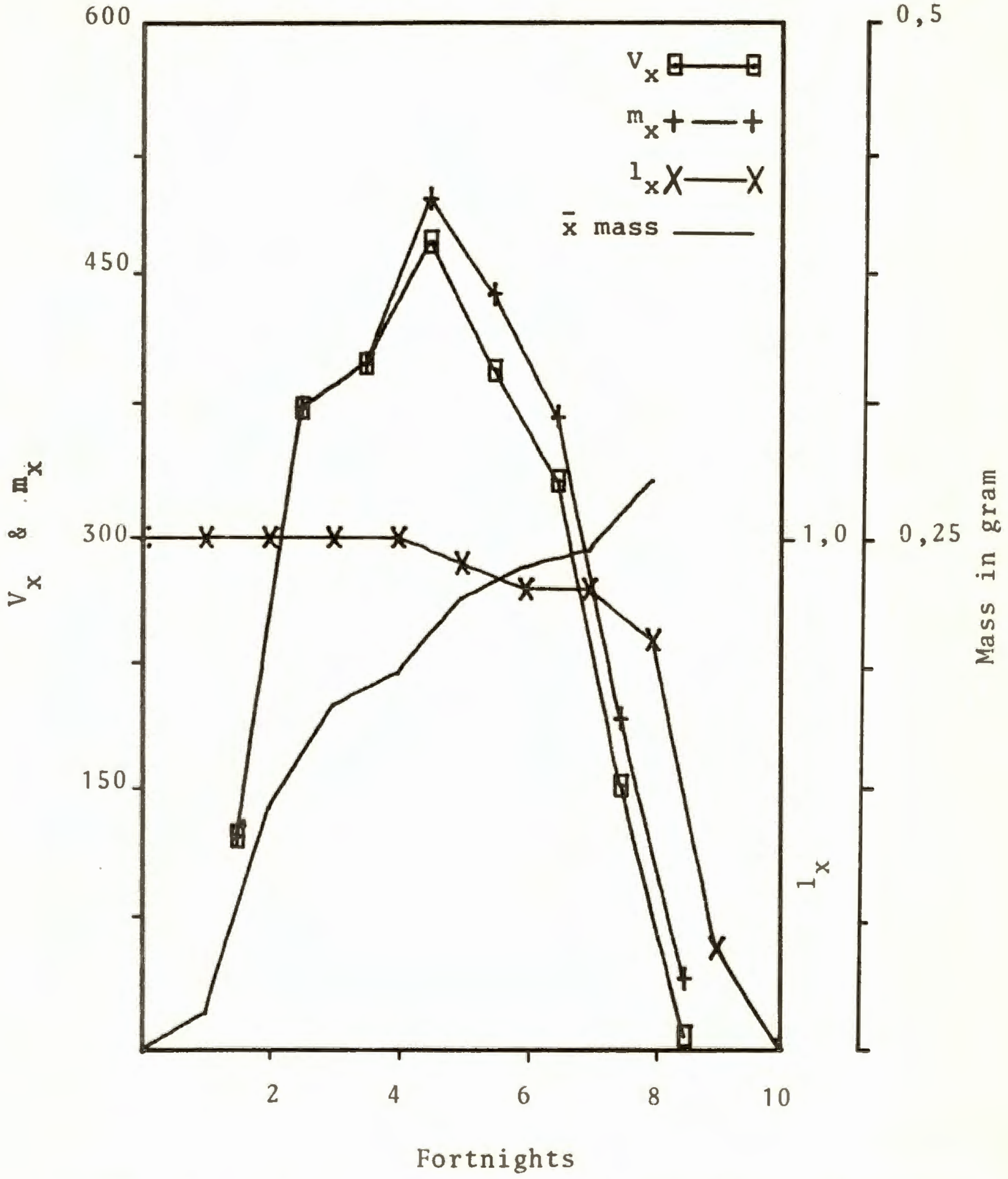


Figure 18. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.pfeifferi* at a conductivity of 250 μS

Table 13 : Life table of *B. pfeifferi* at 310μS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	1 152	20	1,0000	57,6000	57,6000
2,5	5 930	20	1,0000	296,5000	296,5000
3,5	6 091	20	1,0000	304,5500	304,5500
4,5	5 994	20	1,0000	299,7000	299,7000
5,5	4 272	19	0,9500	224,8421	213,6000
6,5	351	13	0,6500	27,0000	17,5500

$R_o = \Sigma V_x = 1\ 189{,}5000$

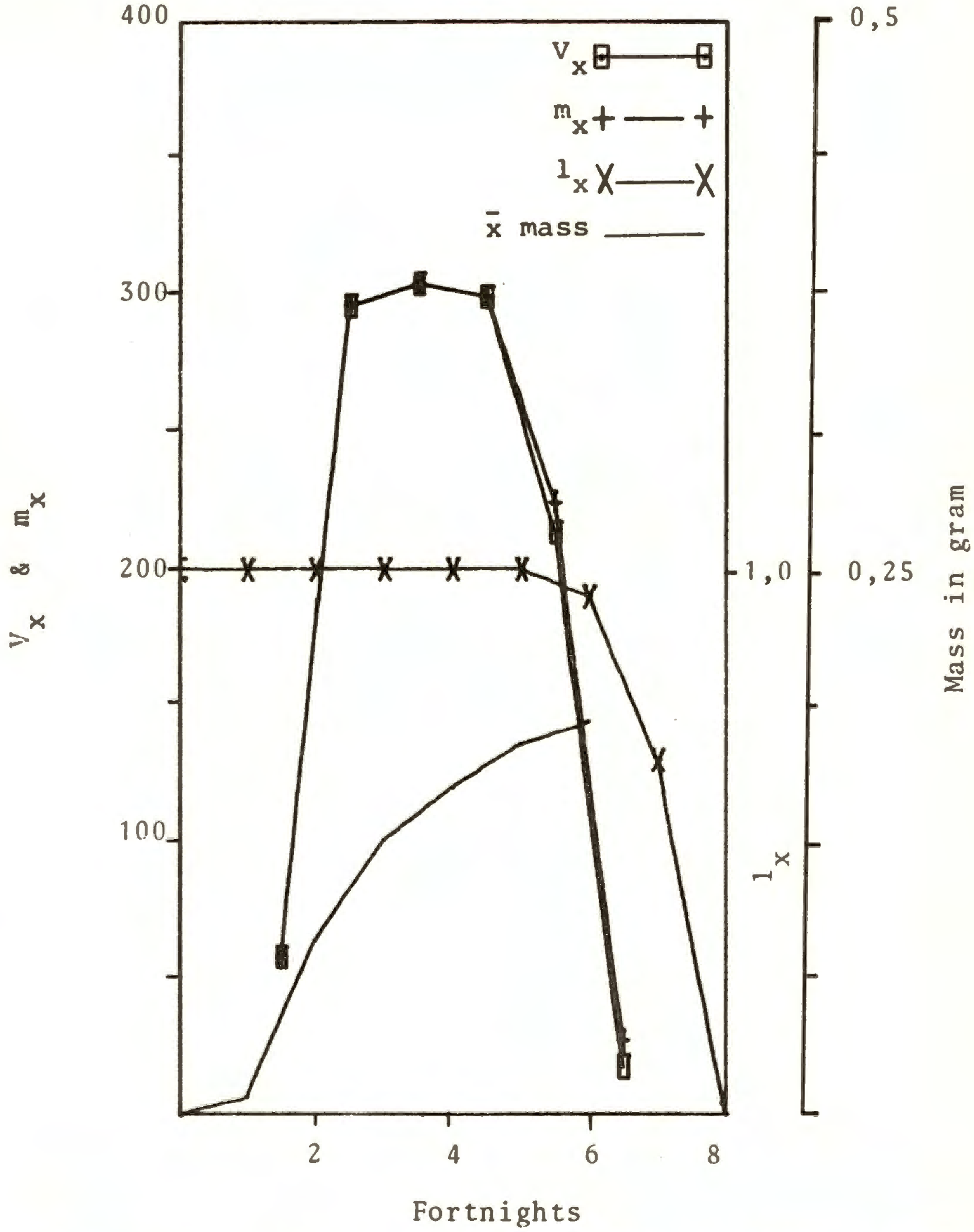


Figure 19. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort *B.pfeifferi* at a conductivity of 310 µS

longer than those of the other two cohorts but despite this a high percentage did hatch. The factors responsible for retarding both hatching and the onset of egg production are not known. Another consequence of the action of these factors was the second lowest R_0 value recorded for *B. pfeifferi* during this experiment.

375 μS

This cohort survived for only five fortnights despite the excellent hatching percentage (table 18). Mortality set in after the second fortnight (table 14 and figure 20) and the whole cohort succumbed over a period of three fortnights. It was, therefore, the cohort with the shortest survival time. Egg production started 20 days after hatching and the hatching time was only seven days. This short hatching period was only equalled by the cohort at 250 μS. This cohort yielded the highest egg output for the first fortnight of any of the cohorts tested. It would, therefore, appear that the factors responsible for the tremendous decline in this cohorts' performance only showed their effect after the second fortnight when, as with *B.(P.) globosus*, the contribution of egg production to the calculation of r_m was already on the decline. The only statistic, therefore, which was seriously influenced was R_0. The fecundity graph (m_x) reached its highest value during the third fortnight. No eggs were produced during the last fortnight.

500 μS

The survival pattern of this cohort was also typical for *B. pfeifferi* (figure 21 and table 15). Mortality was absent for seven fortnights. After this a low rate of mortality occurred for four fortnights and then, as in the other cohorts, it rose sharply resulting in the death of 80% of the entire cohort during the last two fortnights. Egg production started 20 days after hatching and although it reached its highest value during the sixth fortnight, this value was not very much higher than that reached during either the fifth or eighth fortnights.

Table 14 : Life table of *B. pfeifferi* at 375μS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	2 849	20	1,0000	142,4500	142,4500
2,5	4 482	18	0,9000	249,0000	224,1000
3,5	867	13	0,6500	66,6923	43,3500
4,5	0	1	0,0500	0	0

$R_o = \Sigma V_x = 409,9000$

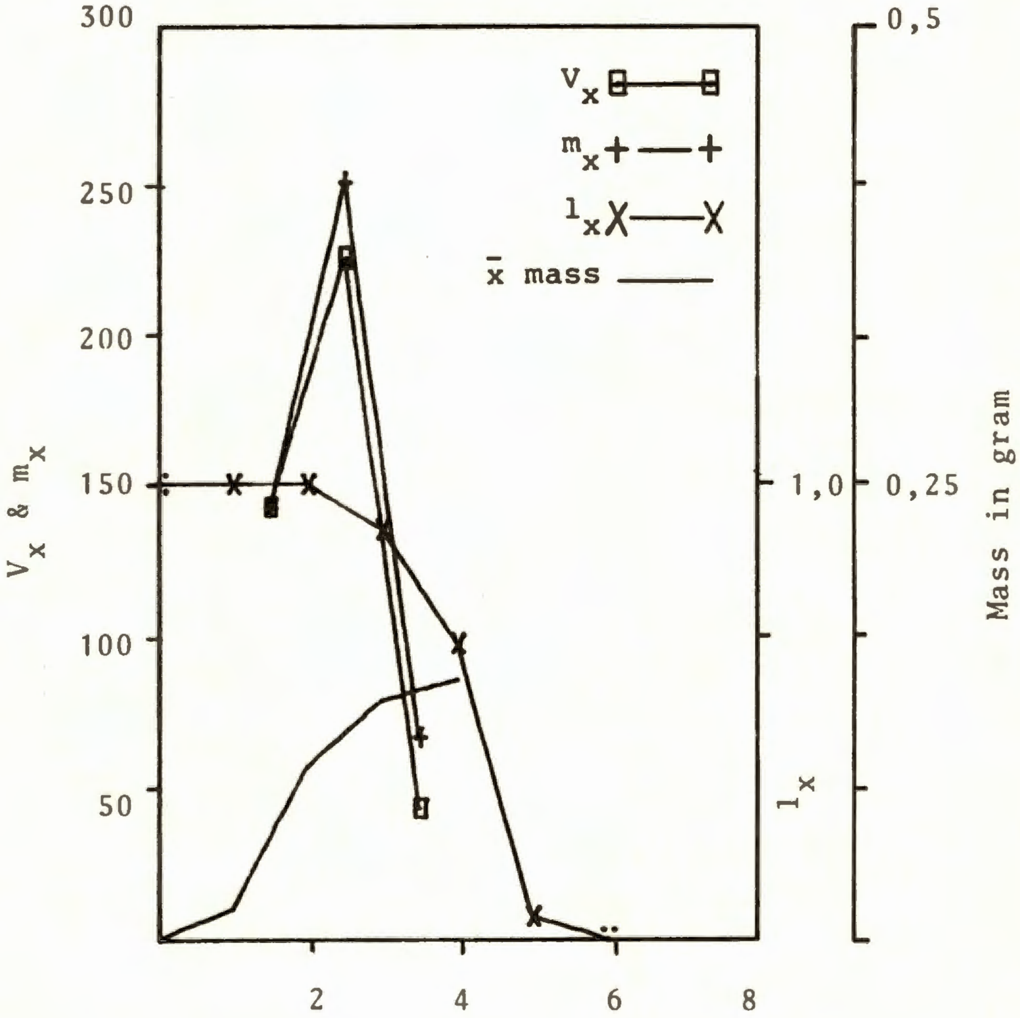


Figure 20. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.pfeifferi* at a conductivity of 375 µS

Table 15 : Life table of *B. pfeifferi* at 500µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	2 276	20	1,0000	113,8000	113,8000
2,5	6 214	20	1,0000	310,7000	310,7000
3,5	6 715	20	1,0000	335,7500	335,7500
4,5	6 855	20	1,0000	342,7500	342,7500
5,5	7 331	20	1,0000	366,5500	366,5500
6,5	6 649	20	1,0000	332,4500	332,4500
7,5	6 484	18	0,9000	360,2222	324,2000
8,5	4 884	17	0,8500	287,2941	244,2000
9,5	4 896	17	0,8500	288,0000	244,8000
10,5	2 956	16	0,8000	184,7500	147,8000
11,5	989	9	0,4500	109,8889	49,4500
12,5	0	1	0,0500	0	0

$R_o = \Sigma V_x = 2\ 812{,}4500$

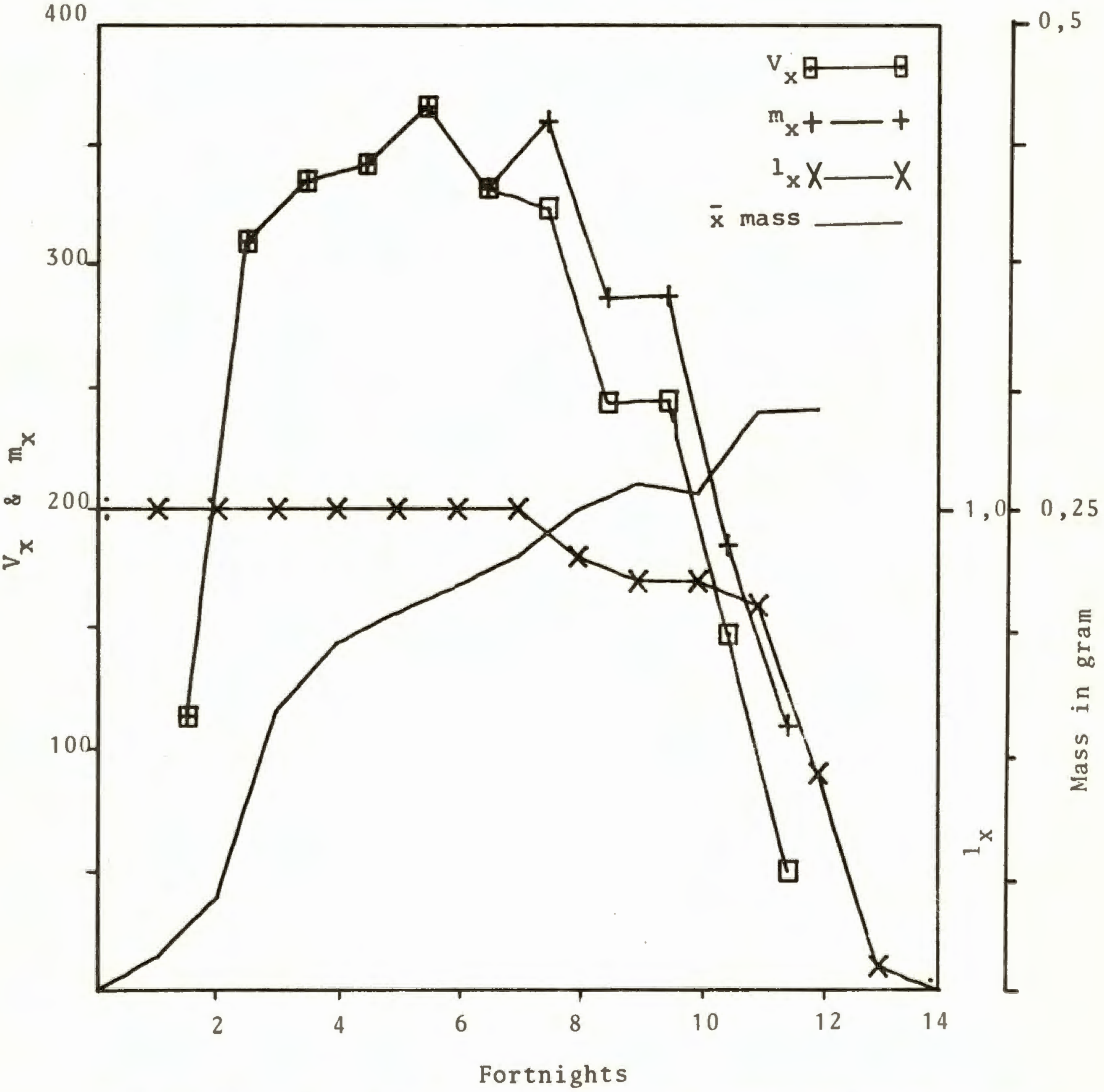


Figure 21. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.pfeifferi* at a conduc= tivity of 500 µS

The m_x graph indicates that instead of a single short peak period of egg production, this cohort maintained a more or less stable high egg production for a few fortnights. Egg production ceased one fortnight before total mortality occurred.

625 µS

The first mortalities occurred after the fourth fortnight and repeated the familiar pattern for *B. pfeifferi* with 85% of the mortalities occurring during the last two fortnights. Egg production started after 31 days which was considerably later than in the other cohorts. The fecundity graph (m_x) reached its highest value during the sixth fortnight, and then declined sharply. Due to the low mortalities the V_x graph closely resembles the m_x graph (figure 22 and table 16). The close agreement between these two graphs was characteristic for all the cohorts of *B. pfeifferi*. This cohort survived for ten fortnights and egg production was maintained throughout.

750 µS

Mortality commenced after the fourth fortnight and remained low for the next five fortnights. After the ninth fortnight it increased and unlike the other cohorts, the terminal mortality period during which 85% of the snails died out lasted for three fortnights (table 17 and figure 23). Egg production started 31 days after hatching and like the cohort at 625 µS the highest value was reached during the sixth fortnight. During the fourth and fifth fortnights a slump in egg production occurred but, as is shown by the m_x graph, it recovered again. From the onset of mortality after the fourth fortnight onwards the V_x graph separated from the m_x graph but still closely resembled it until the seventh fortnight when a sharp increase in the mortality rate ended the resemblance.

Analysis

With the exception of the eggs at 125 µS where only 13,89% of the total hatched, a very high hatching percentage was recorded which differed very little from one cohort to another. The best

Table 16 : Life table of *B. pfeifferi* at 625µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	701	20	1,0000	35,0500	35,0500
2,5	3 704	20	1,0000	185,2000	185,2000
3,5	4 811	20	1,0000	240,5500	240,5500
4,5	6 048	19	0,9500	318,3158	302,4000
5,5	6 743	19	0,9500	354,8947	337,1500
6,5	6 097	19	0,9500	320,8947	304,8500
7,5	3 517	17	0,8500	206,8824	175,8500
8,5	320	12	0,6000	26,6667	16,0000
9,5	150	7	0,3500	21,4286	7,5000

$R_o = \Sigma V_x = 1\ 622{,}5500$

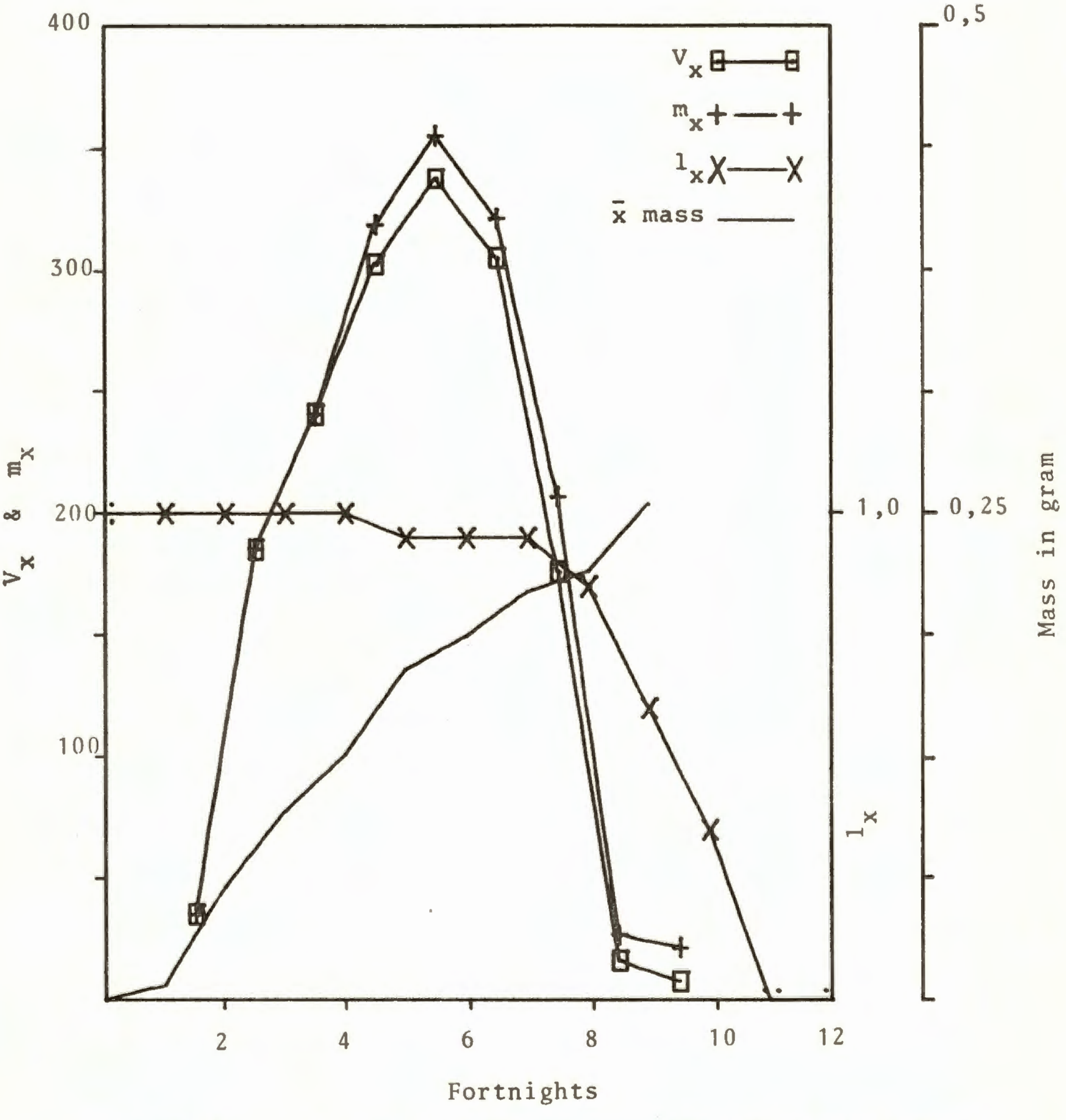


Figure 22. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.pfeifferi* at a conductivity of 625 µS

Table 17 : Life table of *B. pfeifferi* at 750μS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	1 877	20	1,0000	93,8500	93,8500
2,5	7 634	20	1,0000	381,7000	381,7000
3,5	6 137	20	1,0000	306,8500	306,8500
4,5	4 347	19	0,9500	228,7895	217,3500
5,5	8 265	19	0,9500	435,0000	413,2500
6,5	6 149	19	0,9500	323,6316	307,4500
7,5	5 970	18	0,9000	331,6667	298,5000
8,5	5 139	17	0,8500	302,2941	256,9500
9,5	4 279	12	0,6000	356,5838	213,9500
10,5	3 313	11	0,5500	301,1818	165,6500
11,5	0	3	0,1500	0	0

$R_o = \Sigma V_x = 2\ 674{,}5000$

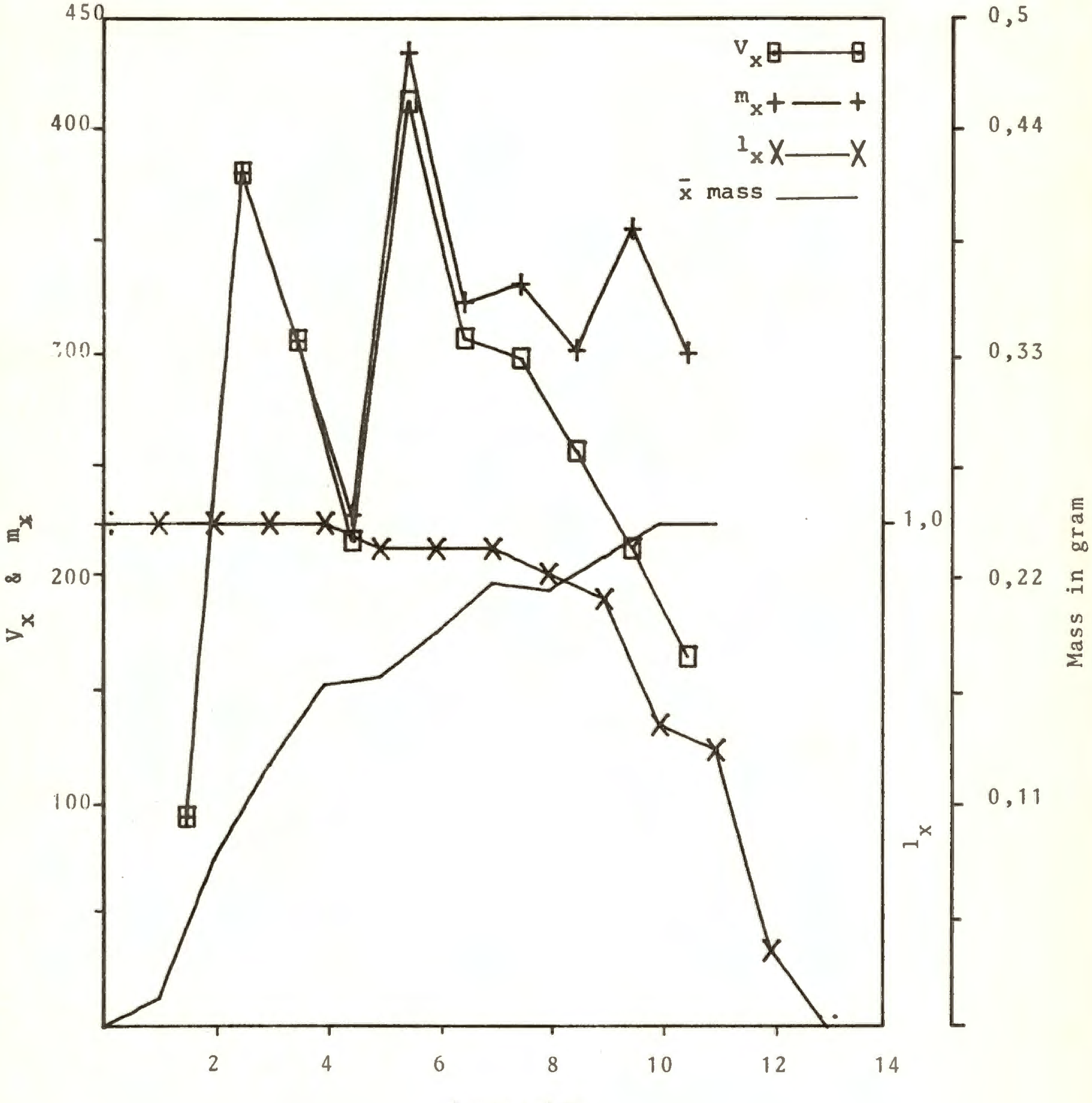


Figure 23. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.pfeifferi* at a conductivity of 750 μS

results were achieved at 375 µS where 98,6 % of the eggs hatched (table 18). At 180 µS where 95% of the eggs hatched the second highest percentage was reached. The hatchlings at 125 µS were unable to survive for more than seven days and in this respect the findings for *B. pfeifferi* corresponded with those for *B.(P.) globosus*. At 50 µS the embryos developed very slowly and although they appeared to be normal in all respects they also died within 14 days like those of *B.(P.) globosus* did at the same conductivity. From the foregoing data it would appear that conductivities above 180 µS and below 750 µS did not affect the ability of eggs to hatch.

The shortest hatching time viz. seven days was registered at conductivities of 250 µS and 375 µS (table 18). It is obvious that in the cohort at 310 µS something must have adversely affected both hatching time and the time preceding oviposition because it could be expected that the performance at 310 µS should lie somewhere between those at 250 µS and 375 µS. The actual values calculated at 310 µS should therefore not be regarded as accurate for *B. pfeifferi*. In fact, a hatching time of approximately seven days and a pre-oviposition interval of approximately 21 days would be more in agreement with the overall pattern which emerges from table 18.

As conductivities decreased from 250 µS, hatching time increased to 20 days at 125 µS. At all conductivities higher than 375 µS the hatching time was also one day longer than at 250 µS. The period preceding egg production was similarly affected. At 180 µS it was 26 and at 625 µS and 750 µS it was 31 days. Both the hatching time and the pre-oviposition period points to a conductivity between 250 and 375 µS as the value most favourable for *B. pfeifferi*.

There was very little difference between the rate of mass increase of the different cohorts (figure 24 and appendix table 15). Although the growth rates of the cohorts at 180 µS and 500 µS were initially lower than those of the other cohorts they improved

Table 18 : Population statistics of cohorts of *B.pfeifferi*.

Conductivity	Hatching time*	Hatching percentage	Start of egg production*	λ	r_m	r_c	R_o	T_c
50μS	-	0	-	-	-	-	-	-
125μS	20	13,89	-	-	-	-	-	-
180μS	8	95	26	12,646	2,5373	1,191	2 966,85	6,713
250μS	7	86,8	20	26,958	3,2943	1,712	2 269,95	4,515
310μS	9	91,7	21	17,824	2,8806	1,859	1 189,50	3,809
375μS	7	98,6	20	28,285	3,3423	2,664	409,90	2,258
500μS	8	93,1	20	25,222	3,2277	1,330	2 812,45	5,972
625μS	8	91,8	31	13,592	2,6095	1,450	1 622,55	5,097
750μS	8	93,5	31	23,093	3,1395	1,333	2 674,50	5,919
875μS	-	0	-	-	-	-	-	-

*In days
r_m - range = 0,8050

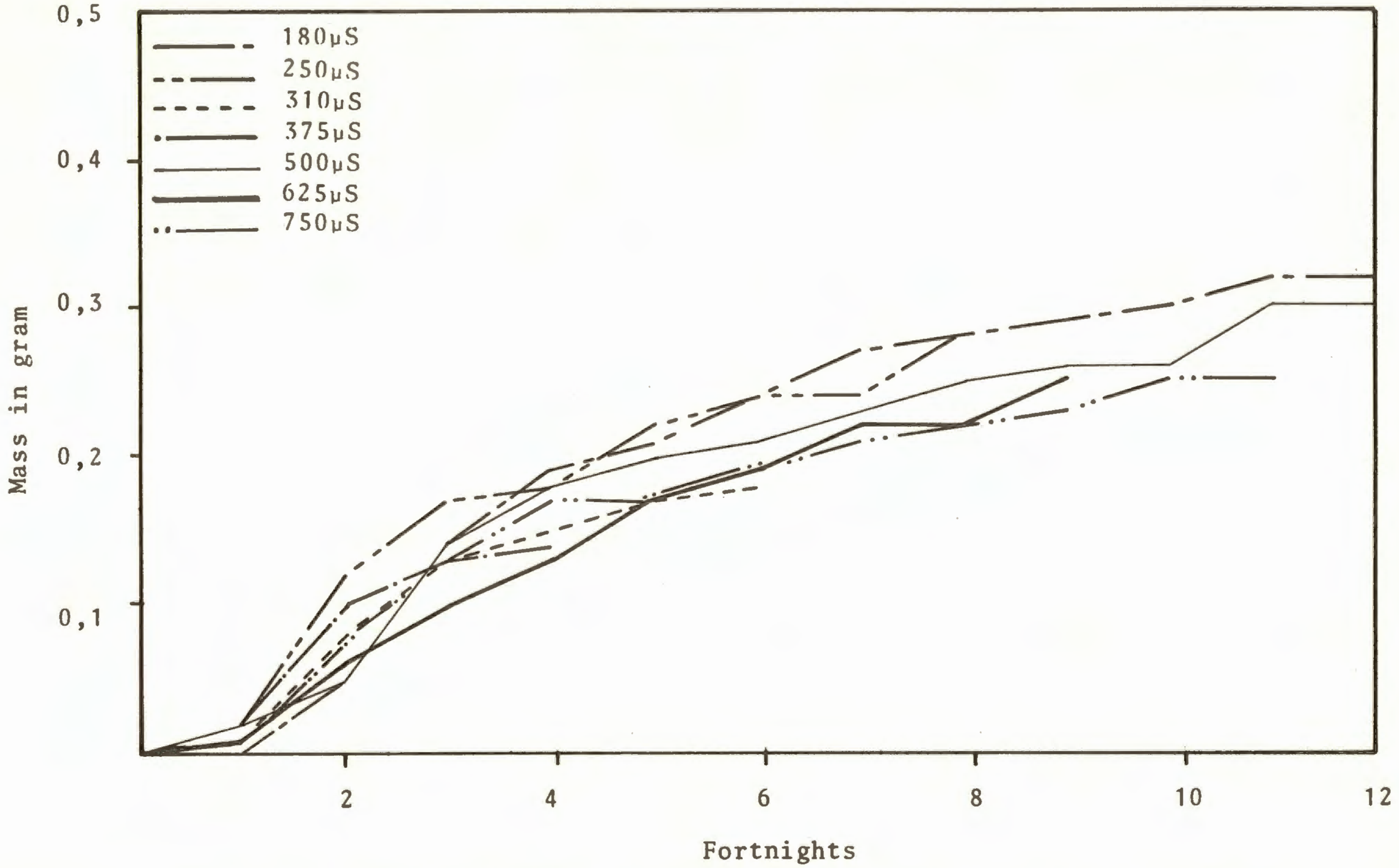


Figure 24. Mean fortnightly mass per snail of cohorts of *B.feifferi* at the various constant conductivities based on the data contained in Appendix table 15

considerably as the experiment proceeded and these two cohorts eventually reached the highest mean mass per snail. The initial slow growth rate of the cohort at 180 µS could possibly be attributed to the apparent detrimental effect of low salinities on juvenile snails. The same explanation might account for the long interval preceding egg production in the same cohort. High salinities apparently had the same effect on growth rate, especially during the first fortnight after hatching. After the first two fortnights the growth rate of the cohort at 180 µS increased considerably and eventually it attained the highest growth rate as well as the highest mean mass per snail of all the cohorts. The latter can partly be attributed to the fact that this cohort as well as the one at 500 µS which reached the second highest mean mass per snail, survived longer than the other cohorts. None of the cohorts produced any eggs before the snails had reached a mean mass of 0,04 g.

There was no obvious correlation between conductivity and longevity within the conductivity ranges evaluated during this experiment. Snails at the lower levels exhibited both the lowest and highest survival rates recorded (figure 25). The three cohorts with the highest mortality rates were those at 375 µS, 310 µS and 250 µS while the highest survival rate was exhibited by the one at 180 µS. The typical *B. pfeifferi* survival pattern of persistent low initial mortalities followed by serious mortalities which ends in total mortality within one or two fortnights is illustrated by the l_x curves in figure 25. At 125 µS survival of the juvenile snails was adversely affected and all hatchlings died a couple of days after hatching.

The reproductive rates (m_x) of the seven cohorts of *B. pfeifferi* are compared in figure 26. In all cohorts egg production commenced during the second fortnight. The reproductive rates of all the cohorts except the one at 375 µS were remarkably similar during the first reproductive fortnight, but after this they diversified considerably. The cohorts at 310 µS and 375 µS reached

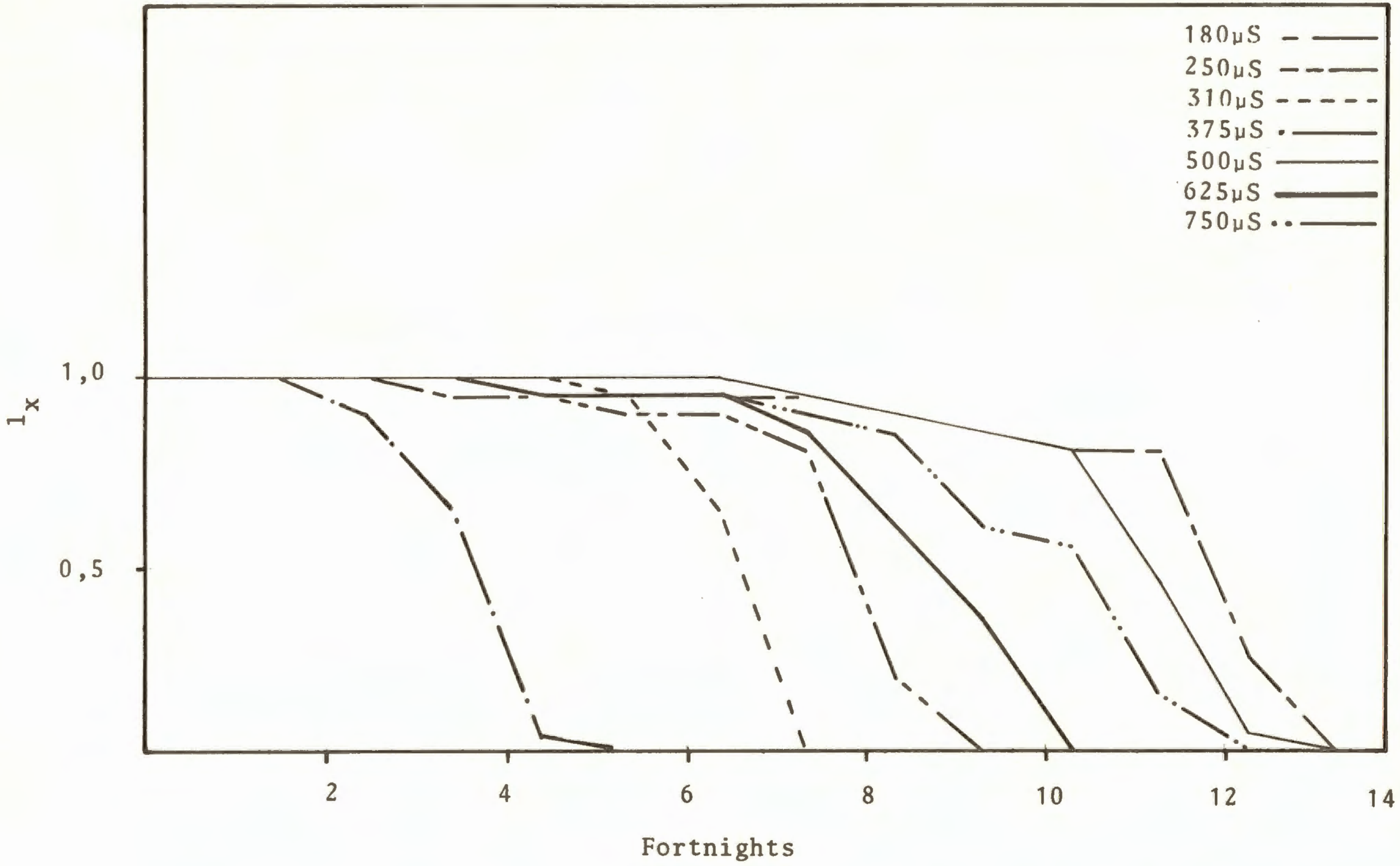


Figure 25. The l_x curves of the cohorts of *B.pfeifferi* at the various constant conductivities

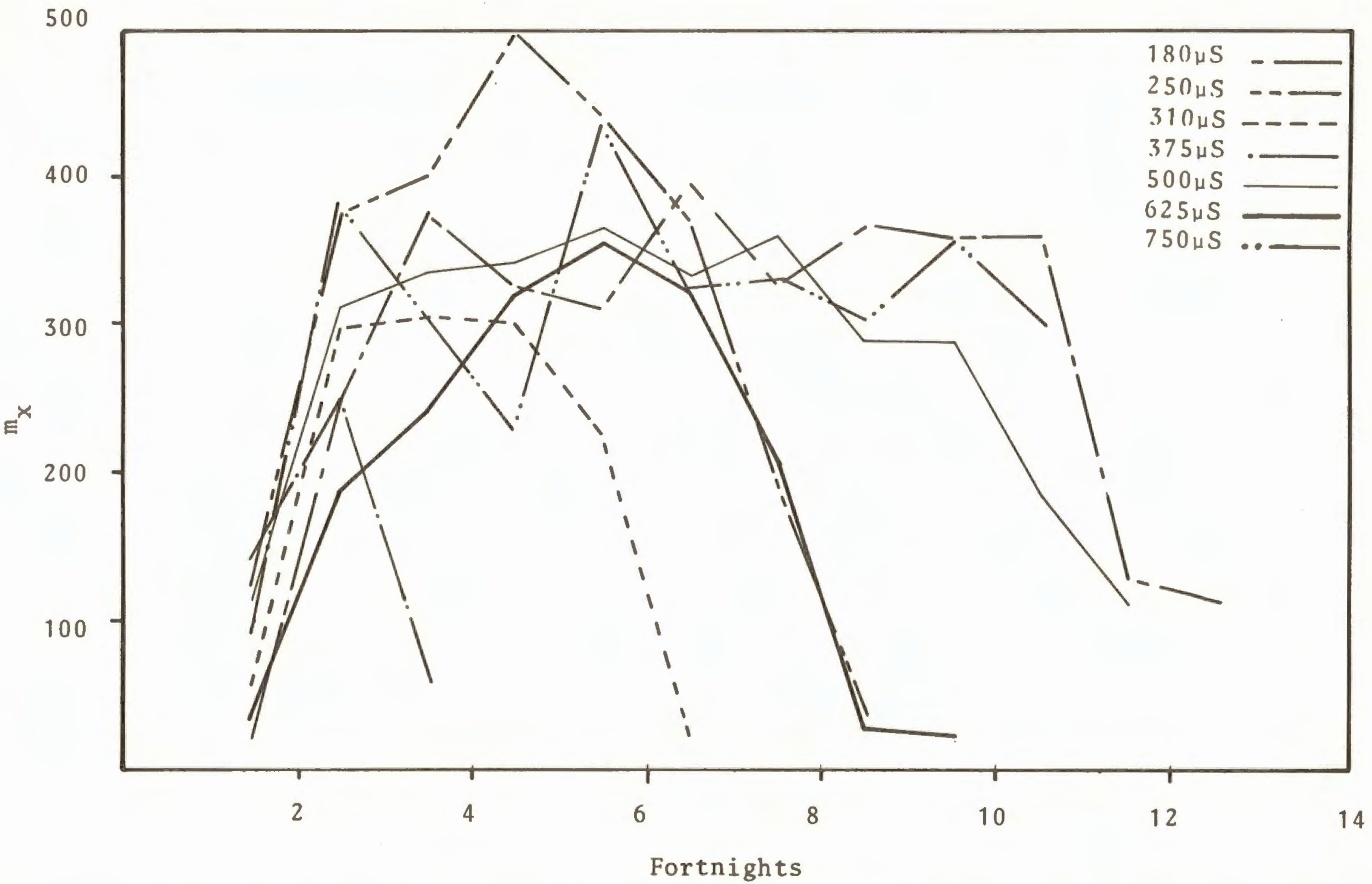


Figure 26. The m_x curves of the cohorts of *B.pfeifferi* at the various constant conductivities

their highest m_x values during the third fortnight. The highest overall m_x value was that of the cohort at 250 µS which was achieved during the fifth fortnight. Although the highest m_x value of the cohort at 180 µS was lower than those of the cohorts at 250 µS and 750 µS it maintained a much longer reproductive period than either of these cohorts as well as the other cohorts except the one at 500 µS which had a reproductive period of one fortnight less than that of the cohort at 180 µS.

Between the conductivities of 180 µS and 750 µS salinity apparently has only a very slight effect on the number of egg clutches produced by a snail. Figure 27, however, reflects no particular pattern in this respect. The cohort at 250 µS which produced the highest mean number of egg clutches per snail was closely followed by those at 180 µS, 375 µS, 500 µS and 750 µS (appendix table 16). The data concerning the mean numbers of eggs per egg clutch (figure 28 and appendix table 17), however, show that the differences between the highest values of the different cohorts were much smaller than those between the mean numbers of egg clutches per cohort (figure 27 and appendix table 16). From this it could be concluded that salinity affected the mean number of egg clutches produced per snail more than it did the mean number of eggs per egg clutch. It, therefore, appears that although conductivity had no significant single effect within the ranges used in this investigation there was a total effect which was revealed by the difference in mean number of egg clutches per snail per cohort. This is supported by the similarity between figures 27 and 26 and in this connection it should be borne in mind that m_x is the product of the mean number of egg clutches per snail and the mean number of eggs per egg clutch. Whereas production of the highest mean number of egg clutches per snail was reached before the highest mean number of eggs per egg clutch the latter was maintained for a much longer period.

The very low initial mortality rates which occurred in all the cohorts were the main reasons for the great similarity between the V_x curves (figure 29) and the m_x curves (figure 26) and

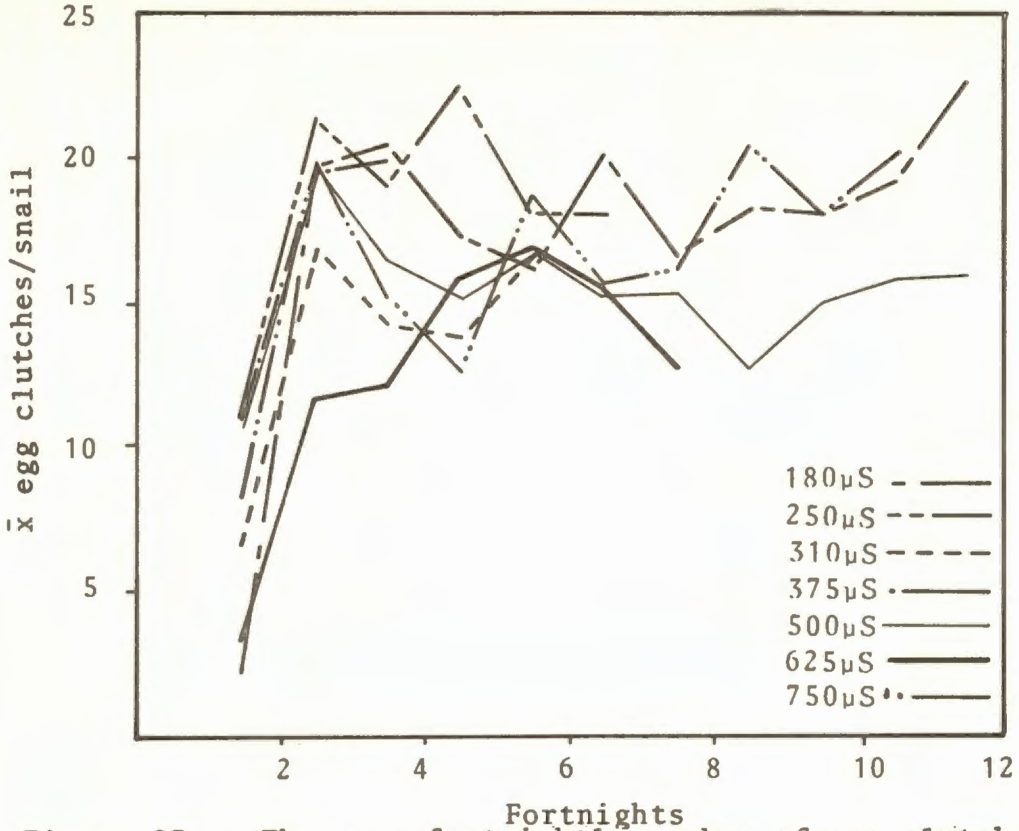


Figure 27. The mean fortnightly number of egg clutches per snail of *B.pfeifferi* at the various con= stant conductivities based on the data con= tained in Appendix table 16

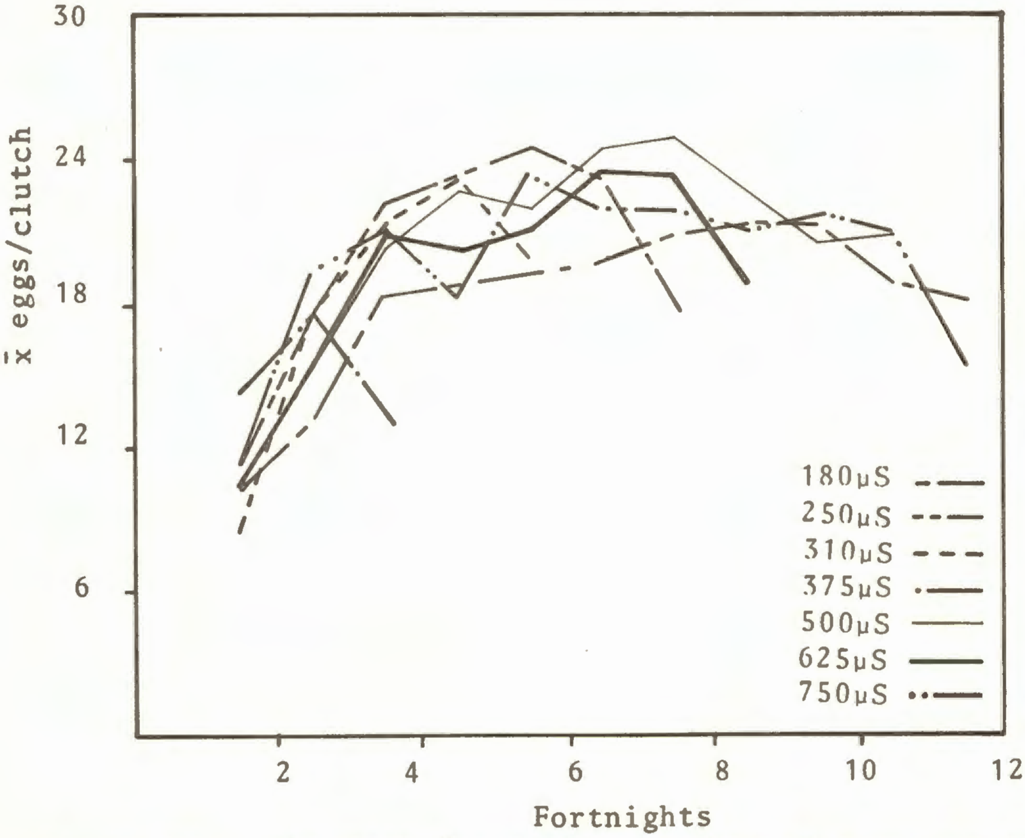


Figure 28. The mean fortnightly number of eggs per egg clutch of *B.pfeifferi* at the various constant conductivities based on thedata contained in Appendix table 17

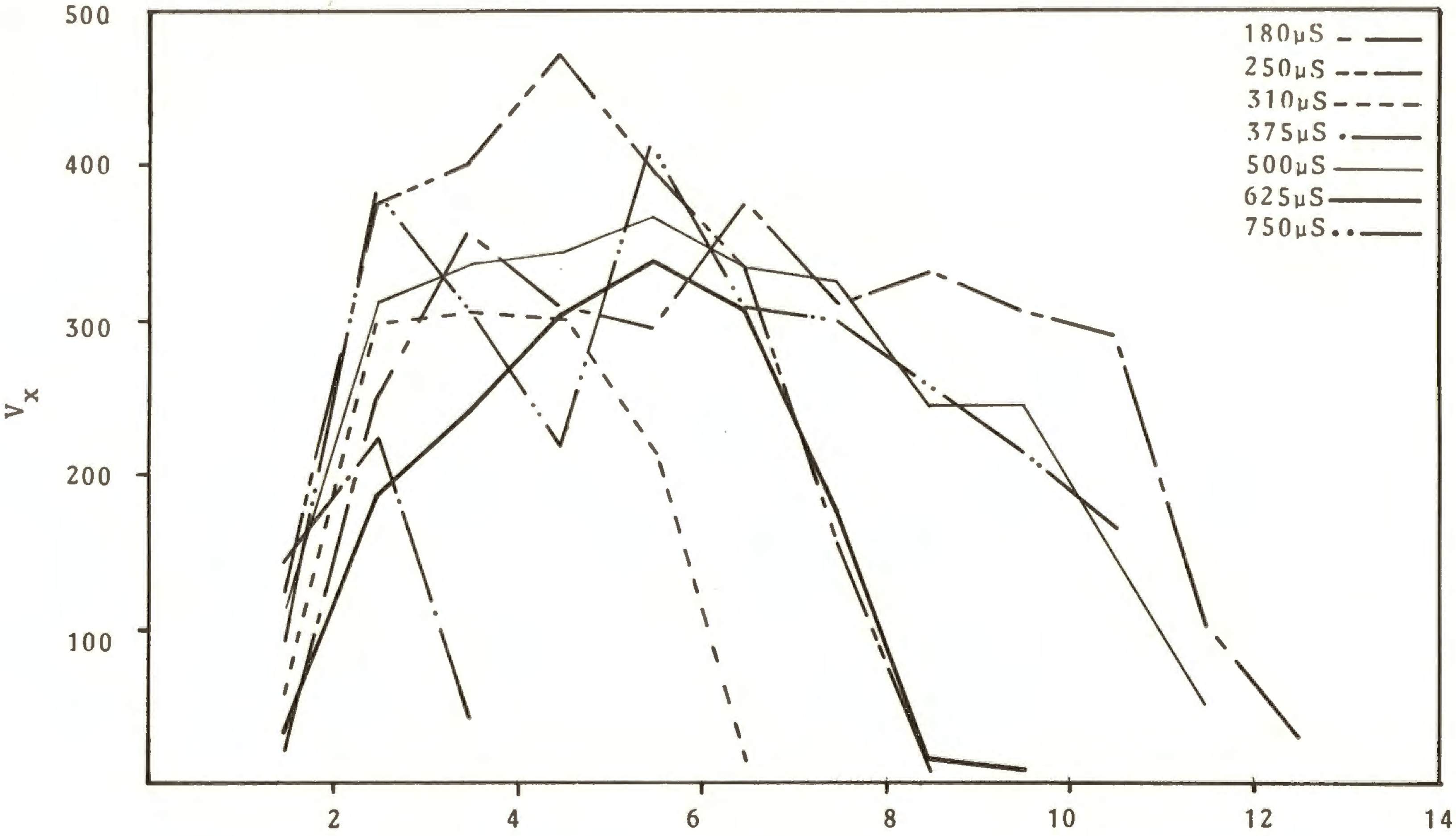


Figure 29. The V_x curves of the cohorts of *B.pfeifferi* at the various constant conductivities

since there were no outstanding differences between the two figures further discussion of the egg curve is not warranted.

The net reproductive rates (R_o) of the different cohorts are presented in table 18, and the accumulation of R_o per fortnight, based on the V_x values is graphically presented in figure 30. The rate of increase in the value of R_o was nearly the same for all the cohorts and it can be seen from figure 30 that the high values reached by the cohorts at 180 µS and 500 µS were mainly the result of better longevity which in turn was the result of low mortality rates. Although the cohort at 250 µS attained the highest rate of increase in the value of R_o it could not equal the eventual R_o values of the cohorts at 180 µS, 500 µS and 750 µS because of its shorter period of survival.

There was a tendency for T_c values to be lower at the moderate than at the extreme salinities. The T_c sequence of the different cohorts was 180 µS > 500 µS > 750 µS > 625 µS > 250 µS > 310 µS > 375 µS. Although the sudden high mortality rate of the cohort at 375 µS must have affected the value of T_c, it may be assumed that the position of this cohort in the T_c sequence is not far from what it would have been, had the survival rate been of the same order as those of the other cohorts.

The intrinsic rates of natural increase (r_m) and the finite rates of increase are presented in table 18. According to the r_m values calculated the cohort at 375 µS with an r_m of 3,3423 was the most successful. This success, however, was not all that outstanding in view of the small differences between r_m values calculated for the other cohorts and that of the cohort at 375 µS. In spite of having the highest R_o value the cohort at 180 µS had the lowest r_m (2,5373). This was the result of a very low reproductive rate during the first reproductive fortnight coupled with the higest T_c value calculated for *B. pfeifferi*. The cohort at 625 µS had the second lowest r_m value despite a better T_c value than the cohorts at both 500 µS

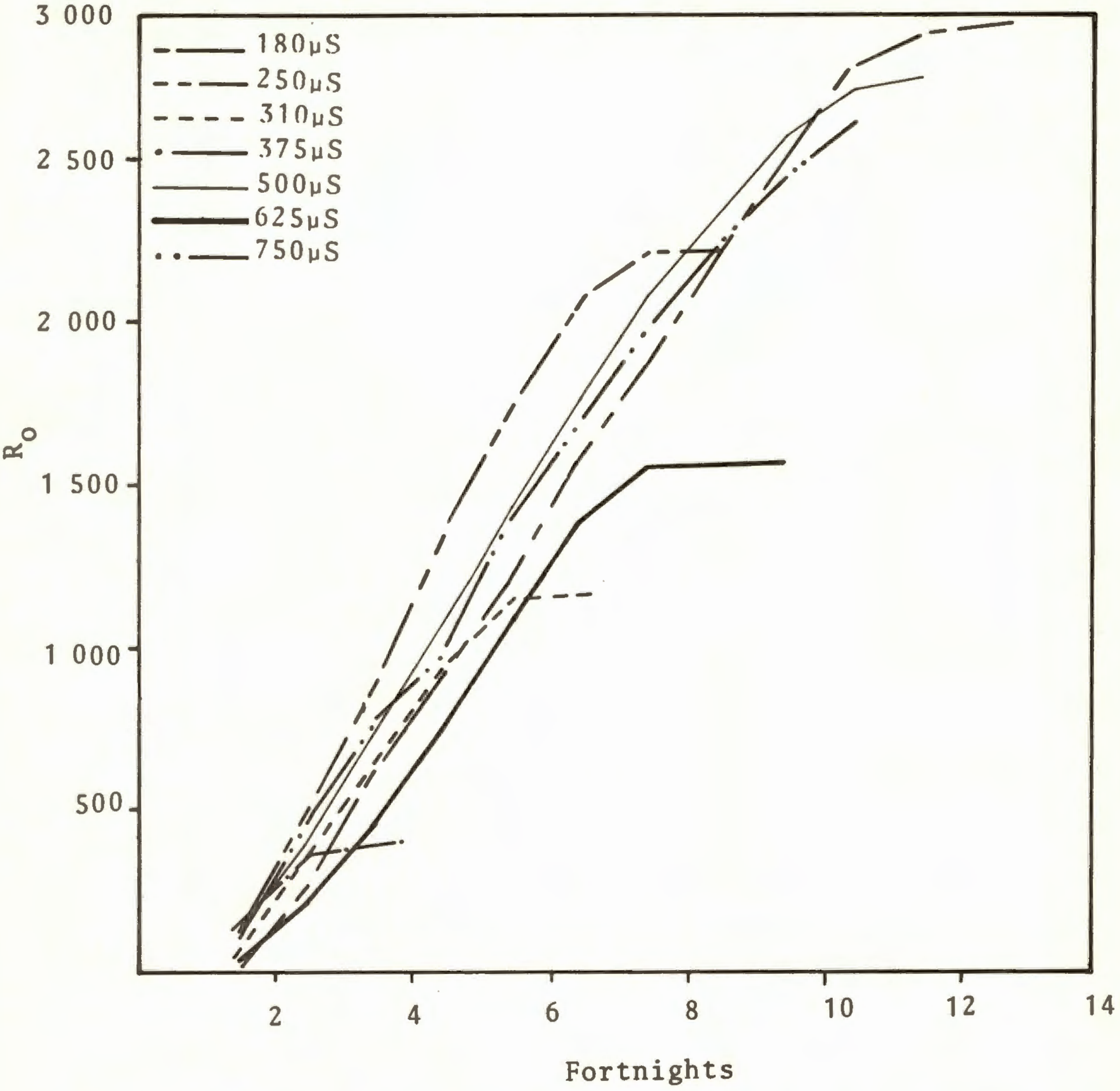


Figure 30. The increase in R_o value per fortnight of the cohorts of *B.pfeifferi* at the various constant conductivities

and 750 µS. In this case it was also handicapped by low egg production during the first reproductive fortnight as well as a net reproductive rate (R_o) that was lower than that of either the cohort at 500 µS or 750 µS. Judging from the r_m values it would be fairly accurate to estimate that the optimum conductivity for *B. pfeifferi* lies somewhere between 310 µS and 500 µS.

The positive r_m values calculated for all the cohorts indicate that *B. pfeifferi* can survive under conditions similar to those created during this experiment and multiply at all conductivities ranging from 180 µS to 750 µS, but most successfully in the region of 310 µS to 500 µS. All values for the finite rate of increase (λ) were higher than one, indicating that an increase in population density can take place under any of these conditions. A comparison of λ values leads to the same conclusion as that reached on the basis of the r_m values.

Jennings et al. (1973) came to the conclusion that the best suited culture water in respect of concentration of total dissolved salts in which to breed *B. pfeifferi* was that with a conductivity of between 350 µS and 400 µS. The r_m values calculated for the present experiments indicate this to be an accurate assumption and that the optimum conductivity for this species is probably in the region of 375 µS.

3.4 Life tables of *L. natalensis*

125 µS

Only 45,45% of the eggs hatched. During the first three fortnights the hatchlings grew so slowly that, at the end of the first fortnight, they could still not be weighed (appendix table 18). After the second fortnight mortalities commenced and remained very high during the following two fortnights (table 19 and figure 31). The m_x curve shows two peaks, one during the sixth and a higher one during the eighth fortnight. The latter

Table 19 : Life table of *L. natalensis* at 125µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	0	11	0,5500	0	0
3,5	258	5	0,2500	51,6000	12,9000
4,5	1 315	5	0,2500	263,0000	65,7500
5,5	1 777	5	0,2500	355,4000	88,8500
6,5	1 088	4	0,2000	272,0000	54,4000
7,5	640	1	0,0500	640,0000	32,0000
8,5	87	1	0,0500	87,0000	4,3500

$R_o = \Sigma V_x = 258{,}2500$

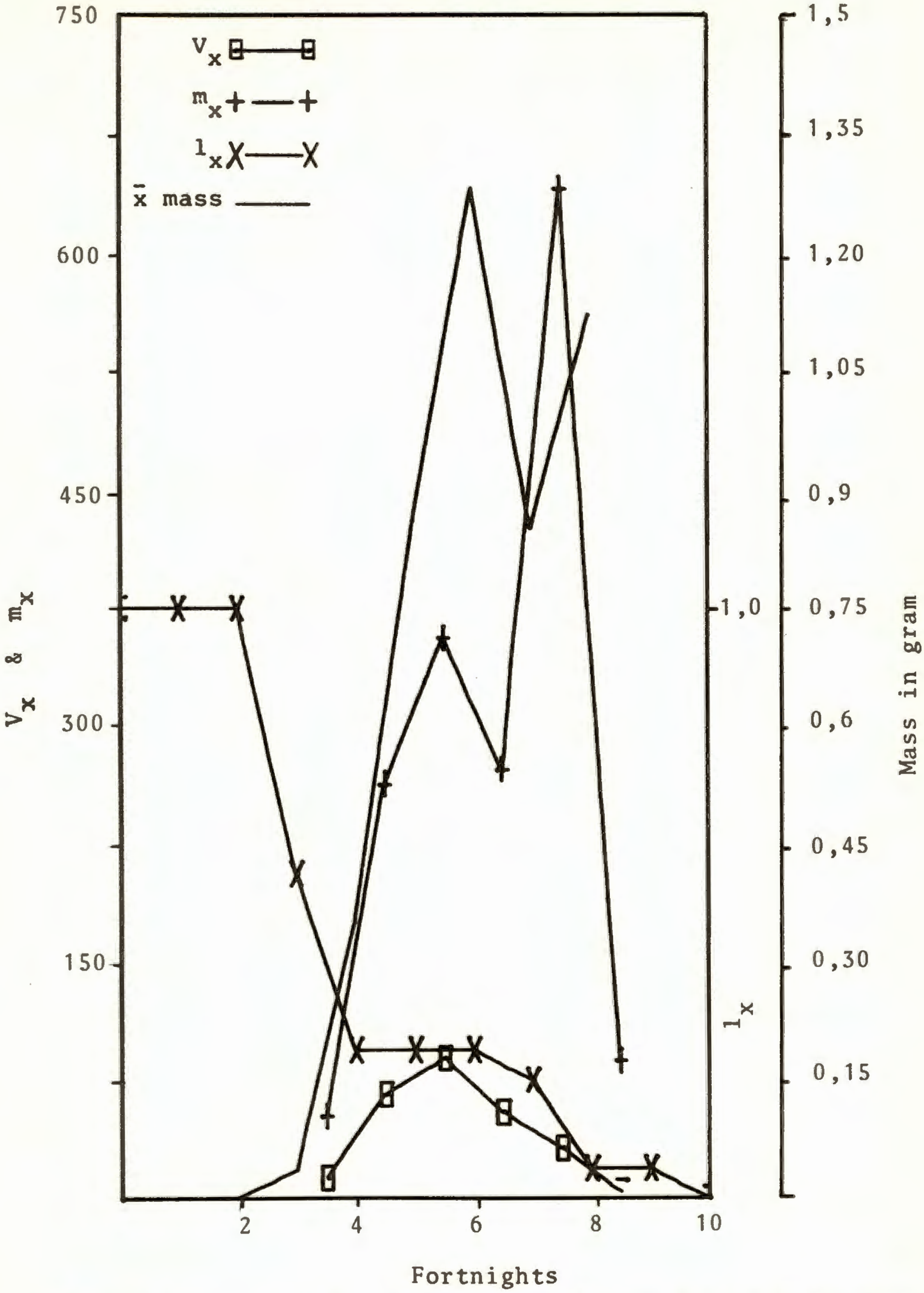


Figure 31. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *L.natalensis* at a conductivity of 125 µS

peak is somewhat misleading as it represents the egg production of only one extremely prolific snail which was, however, so penalized by the low survival rate that this peak is not repeated in the V_x curve. It is clear from the V_x curve that the most significant m_x peak was the one which occurred during the sixth fortnight. The snails reached their highest mean individual mass during the sixth fortnight and the drop in the mass curve during the seventh fortnight, followed by the rise one fortnight later, was the result of fluctuations in the mean mass caused by the deaths of either large or small snails. This wrongly suggests either negative or positive growth rates and is an example of what was discussed earlier on where the influence of mortality on the comparison of growth rates was dealt with.

Egg production started 49 days after hatching and at this stage only five snails contributed to the calculation of m_x (tables 24 and 19). Although the survival period of nine fortnights appears to be within the normal life expectation for *L. natalensis*, only one snail survived during the last two fortnights. Therefore the very high mortality rate throughout the experiment did have a negative effect on the results.

180 μS

Egg production started 37 days after the snails had hatched and continued for six fortnights. No eggs were produced during the last fortnight. The fecundity (m_x) curve reached its highest value during the sixth fortnight. Early mortalities caused the V_x curve to diverge considerably from the m_x curve from the second fortnight onwards. The highest V_x value of 297,05, reached during the sixth fortnight, was considerably higher than the highest V_x value (88,85) reached by the cohort at 125 μS. The highest mean individual mass was recorded during the seventh fortnight (figure 32 and table 20).

Table 20 : Life table of *L. natalensis* at 180µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	315	18	0,9000	17,5000	15,7500
3,5	1 576	14	0,7000	112,5714	78,8000
4,5	4 895	13	0,6500	376,5385	244,7500
5,5	5 941	12	0,6000	495,0833	297,0500
6,5	2 485	12	0,6000	207,0833	124,2500
7,5	1 103	12	0,6000	91,9167	55,1500
8,5	0	2	0,1000	0	0

$R_o = \Sigma V_x = 815,7500$

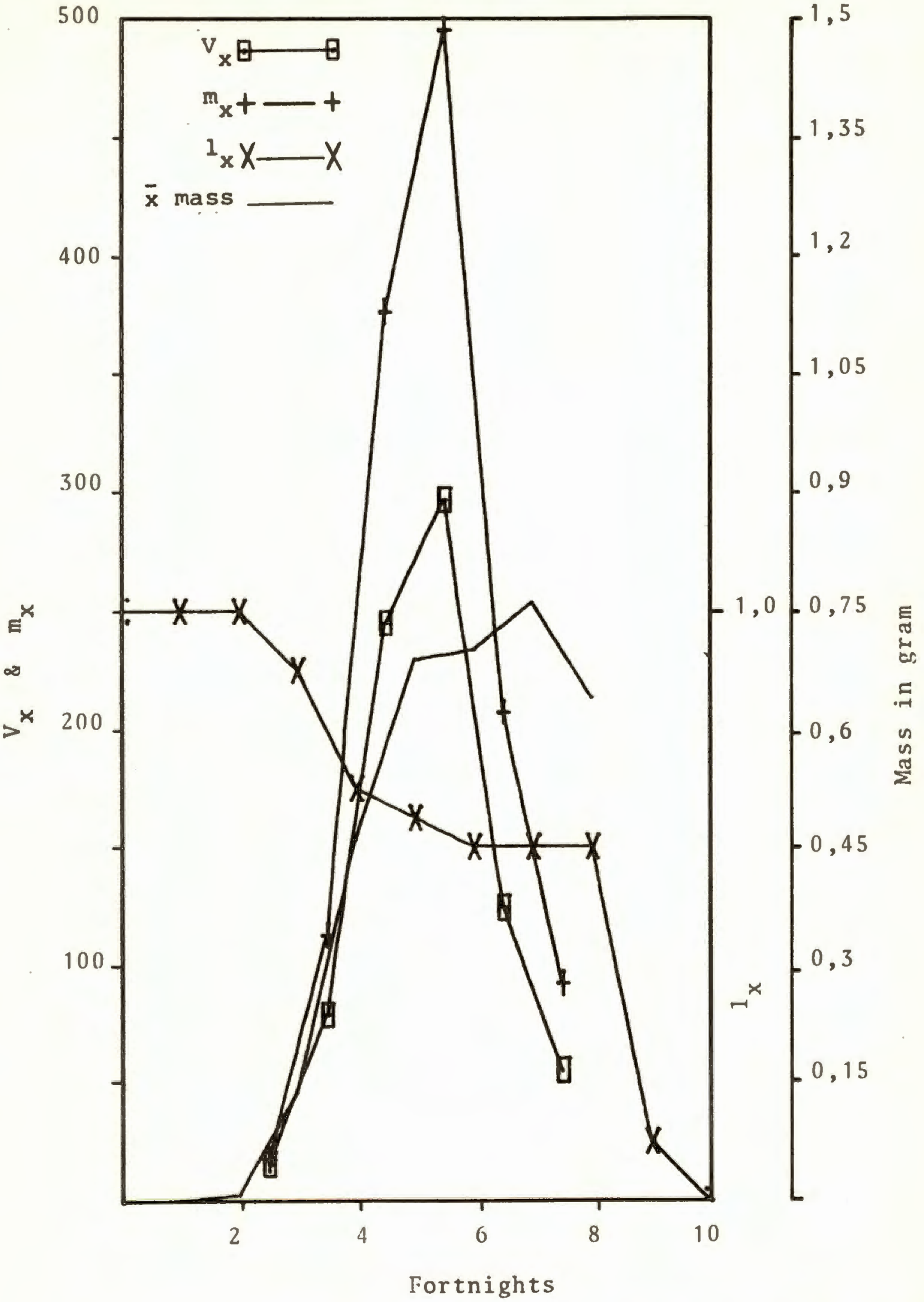


Figure 32. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *L.natalensis* at a conductivity of 180 µS

250 µS

This cohort, with a hatching percentage of 95,70% and a pre-egg laying period of 25 days, attained the best overall performance. The snails survived for a total of eight fortnights showing a very low mortality rate for the first seven periods (figure 33 and table 21). For this reason the m_x and V_x curves are very similar in shape. The fecundity curve reached its highest value during the fifth fortnight, one fortnight earlier than the cohorts at 125 µS and 180 µS. The highest m_x and V_x values reached by this cohort were both considerably higher than those of the other four cohorts of *L. natalensis*. The high m_x value was, however, only maintained for one fortnight after which it dropped sharply due to a decline in the reproductive rate. The reproductive period of this cohort was seven fortnights which was the longest recorded for any cohort of the species concerned.

310 µS

A hatching time of seven days, the shortest for this species, was recorded for this cohort (table 24). The period preceding egg production was 31 days which was the second shortest time for *L. natalensis*, the shortest being that of the cohort at 250 µS. Mortalities started after the fifth fortnight which was considerably later than in the other cohorts but as can be seen from the l_x curve in figure 34 the mortality period lasted for three fortnights. The fecundity curve reached its highest value during the sixth fortnight (table 22 and figure 34), one fortnight later than that of the cohort at 250 µS. The highest m_x value was, however, much lower than that of the cohorts at 125 µS, 180 µS and 250 µS. The snails survived for eight fortnights and reproduced for six fortnights.

375 µS

The hatching time at this conductivity was 10 days and egg production started 32 days after hatching (table 24). The m_x curve

Table 21 : Life table of *L. natalensis* at 250µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	5	20	1,0000	4,0000	4,0000
2,5	2 273	19	0,9500	119,6316	113,6500
3,5	8 809	18	0,9000	489,3889	440,4500
4,5	11 875	18	0,9000	659,7222	593,7500
5,5	6 573	18	0,9000	365,1667	328,6500
6,5	2 703	18	0,9000	150,1667	135,1500
7,5	126	12	0,6000	10,5000	6,3000

$R_o = \Sigma V_x = 1\ 621{,}9500$

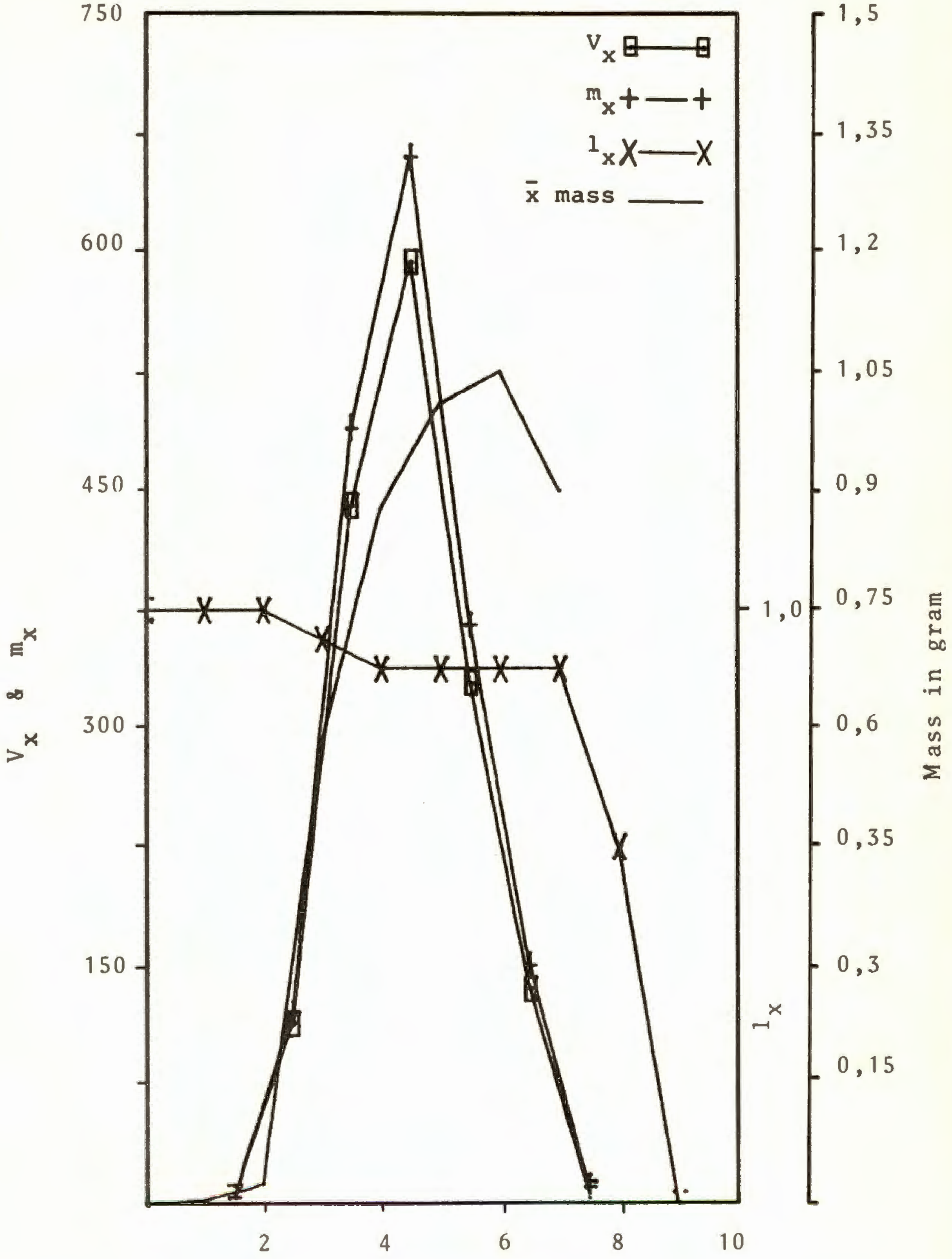


Figure 33. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *L.natalensis* at a conductivity of 250 µS

Table 22 : Life table of *L. natalensis* at 310µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	158	20	1,0000	7,9000	7,9000
3,5	2 844	20	1,0000	142,2000	142,2000
4,5	2 551	20	1,0000	127,5500	127,5500
5,5	3 220	11	0,5500	292,7273	161,0000
6,5	836	7	0,3500	119,4286	41,8000
7,5	44	2	0,1000	22,0000	2,2000

$R_o = \Sigma V_x = 482,6500$

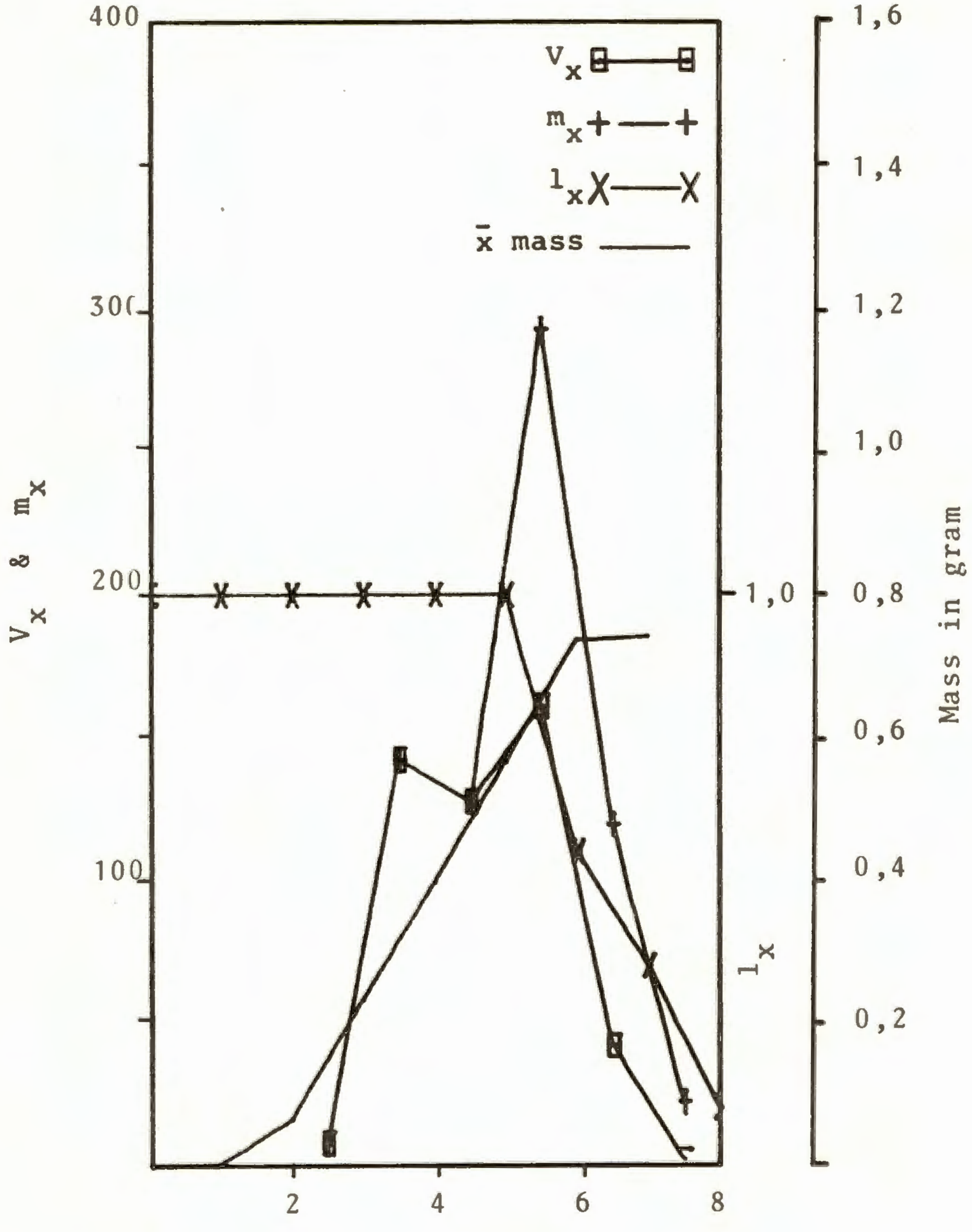


Figure 34. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *L.natalensis* at a conductivity of 310 µS

Table 23 : Life table of *L. natalensis* at 375μS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 003	19	0,9500	52,7895	50,1500
3,5	3 900	17	0,8500	229,4118	195,0000
4,5	1 647	15	0,7500	109,8000	82,3500
5,5	53	6	0,3000	8,8333	2,6500

$R_o = \Sigma V_x = 330{,}1500$

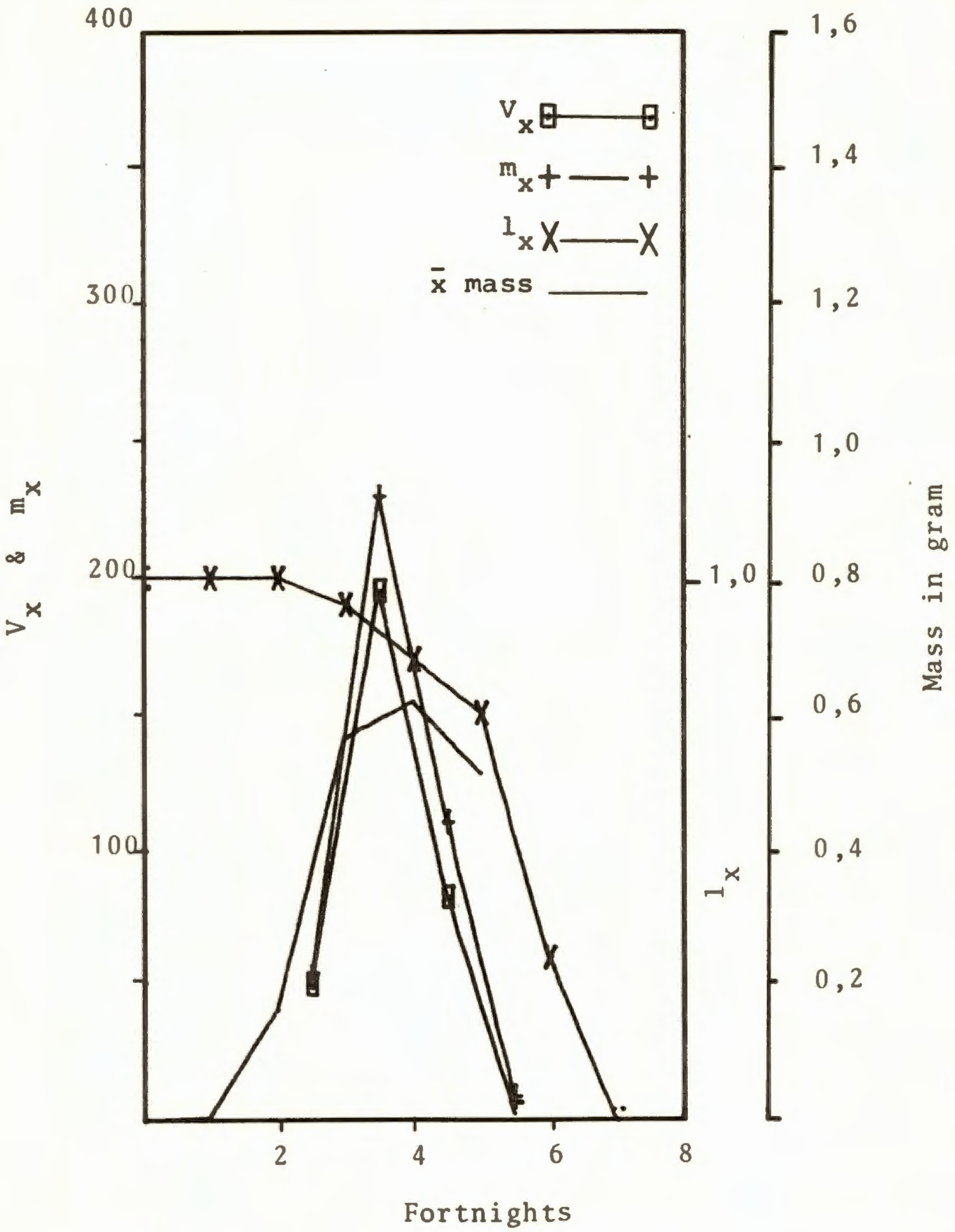


Figure 35. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *L.natalensis* at a conductivity of 375 µS

reached its highest value during the fourth fortnight (table 23 and figure 35) and reproduction lasted for only four fortnights thus making this the cohort with the shortest reproductive period. The snails in this cohort produced more eggs during the first reproductive fortnight than any of the cohorts of *L. natalensis* but the egg production during the subsequent fortnights was lower than that of the cohort at 250 µS.

Analysis

It is clear from the data contained in table 24 that salinity above and below certain concentrations surpressed the hatching ability of eggs. At 250 µS, 95,70% of the eggs hatched but as conductivities increased to 500 µS or decreased to 125 µS the hatching percentage tapered off to 58,14% and 45,45% respectively. At 50 µS hatching ability was so adversely affected that no eggs hatched at all. Salinity had a similar effect on both hatching time and the length of the period preceding egg production. At 310 µS, where the third best hatching percentage was achieved, the eggs hatched in seven days. At 250 µS where the highest hatching percentage occurred this period was ten days thus equalling the hatching time of the eggs at 180 µS where the second best hatching percentage was recorded. At 125 µS and 500 µS hatching time was 13 and 12 days respectively. At 250 µS 25 days passed between hatching and the production of the first eggs. This period increased to 49 days at 125 µS and to 32 days at 375 µS. Although the shortest hatching time occurred at 310 µS it was obvious that the conductivity best suited for both successful hatching and rapid development to maturity was 250 µS. Although 58,14% of the eggs at 500 µS hatched within 12 days, these hatchlings were unable to survive and all died within a couple of days of birth. At 50 µS embryos developed in the egg capsules but were unable to hatch and consequently died.

Table 24 : Population statistics of cohorts of *L.natalensis*.

Conductivity	Hatching time*	Hatching percentage	Start of egg production*	λ	r_m	r_c	R_o	T_c
50µS	-	0	-	-	-	-	-	-
125µS	13	45,45	49	3,005	1,1003	0,982	258,25	5,655
180µS	10	94,91	37	4,668	1,5407	1,280	815,75	5,236
250µS	10	95,70	25	8,464	2,1358	1,657	1 621,95	4,462
310µS	7	88,10	31	4,634	1,5335	1,317	482,65	4,693
375µS	10	81,08	32	5,924	1,7791	1,605	330,15	3,614
500µS	12	58,14	-	-	-	-	-	-

*In days

r_m-range = 1,0355

The highest mean individual mass reached by *L. natalensis* was 1,2897 g at 125 µS during the sixth fortnight (figure 36 and appendix table 18). During the eighth fortnight the only survivor in this cohort had a mass of 1,1286 g. Although the cohort at 375 µS showed the highest initial growth rate it was overtaken after the third fortnight by the cohort at 250 µS which eventually reached the second highest mean mass per snail during the sixth fortnight. The cohort at 125 µS reached the highest mean mass despite its lowest growth rate during the first four fortnights. This indicates growth inhibition by low salinities. There are no noteworthy differences between the mass curves of the cohorts at 180 µS and 310 µS. Unlike the three aspects discussed above there was no apparent pattern in the way growth of *L. natalensis* was affected by the different conductivities except for the inhibition of juvenile growth at the lower conductivity ranges. Once a certain viability was attained, however, conductivity within the ranges investigated during this experiment had no effect on growth as can be seen by the high mass reached by snails at 125 µS, 250 µS and 310 µS. Hatchlings at conductivities of 250 µS, 310 µS and 375 µS grew much quicker with the best growth rates recorded at the two higher conductivities. The higher conductivity ranges, therefore, apparently favoured higher growth rates during the first few fortnights.

The cohort at 250 µS started producing eggs when the mean individual mass per snail was 0,0255 g. This value, however, is much lower than those at which the snails in the other cohorts had started producing eggs.

The cohort at 375 µS survived for only six fortnights despite low mortality rates during the first four fortnights (figure 37). The sudden mass mortalities that took place here also occurred in the cohorts of the other three species at this conductivity. It therefore seems reasonable to assume that this must have been caused by certain changes in the conditions under which

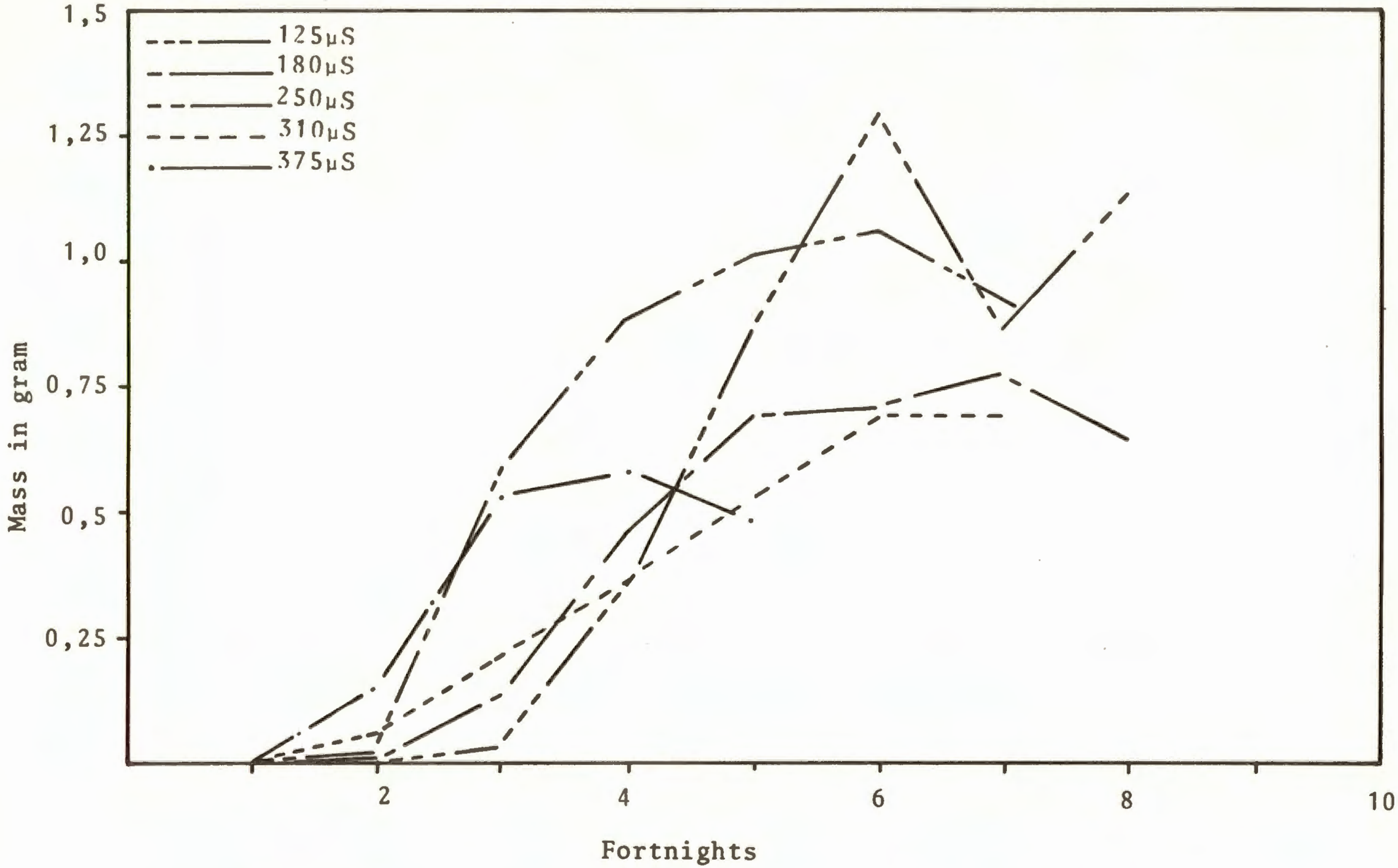


Figure 36. Mean fortnightly mass per snail of the cohorts of *L.natalensis* at the various constant conductivities based on the data contained in Appendix table 18

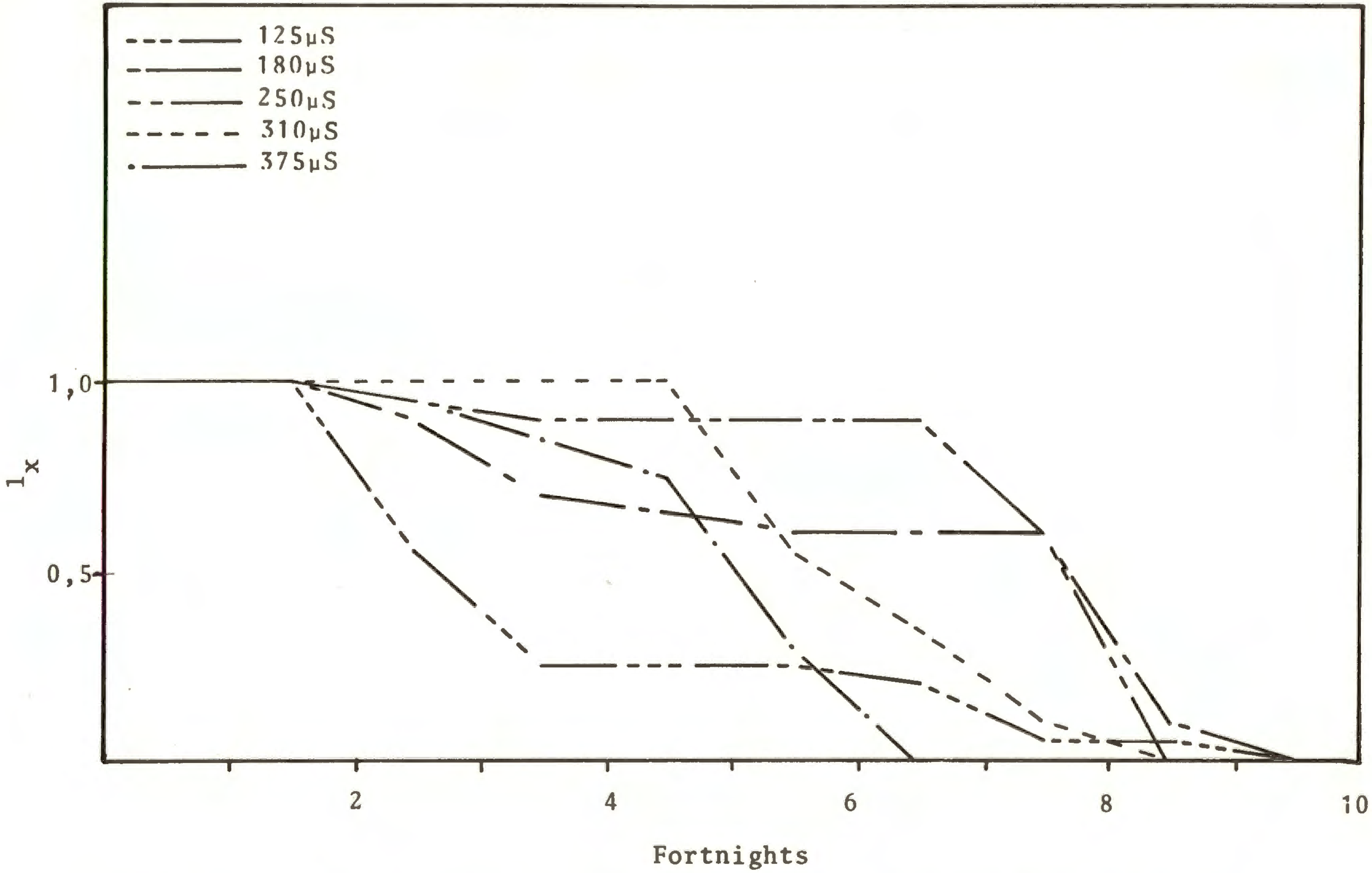


Figure 37. The l_x curves of the cohorts of *L.natalensis* at the various constant conductivities

the snails at this conductivity were being kept. Unfortunately the exact nature of these changes could not be established.

With the exception of this cohort survival was as was expected for *L. natalensis* under intensive artificial breeding conditions and the remaining cohorts died within a fortnight of each other. The snails at 125 μS survived for nine fortnights despite initial high mortalities.

Egg production started one fortnight earlier and one fortnight later in the cohorts at 250 μS and 125 μS respectively than in the three cohorts at 180 μS, 310 μS and 375 μS (figure 38). Of all these the cohort at 250 μS attained the highest reproductive rate as well as the highest value for m_x. The m_x curves in figure 38 all display sharp peaks which indicate that a high mean egg production per snail per fortnight (m_x) was only achieved for one fortnight. Although the cohort at 375 μS produced the highest number of eggs during the first reproductive period and also had a very high initial reproductive rate, the serious mortalities probably prevented it from realizing its true reproductive potential. The high egg production of the sole survivor during the eighth fortnight was responsible for the second peak of the m_x curve. This snail was most probably the main contributor towards the higher total egg production during the seventh fortnight but as a result of the poor egg production of the other three snails, the m_x curve declined during this period. During the eighth fortnight this handicap was removed by the death of these three snails resulting in the second peak of the m_x curve (table 19 and figures 31 and 38). This illustrates how the death of a large percentage of the members of a cohort as well as individual differences in egg production can affect the shape of the m_x curve.

There is a reasonable resemblance between the shapes of the curves in figure 39 and figure 38 and also between the curves of the cohorts at 125 μS, 180 μS and 250 μS in figures 39 and 40.

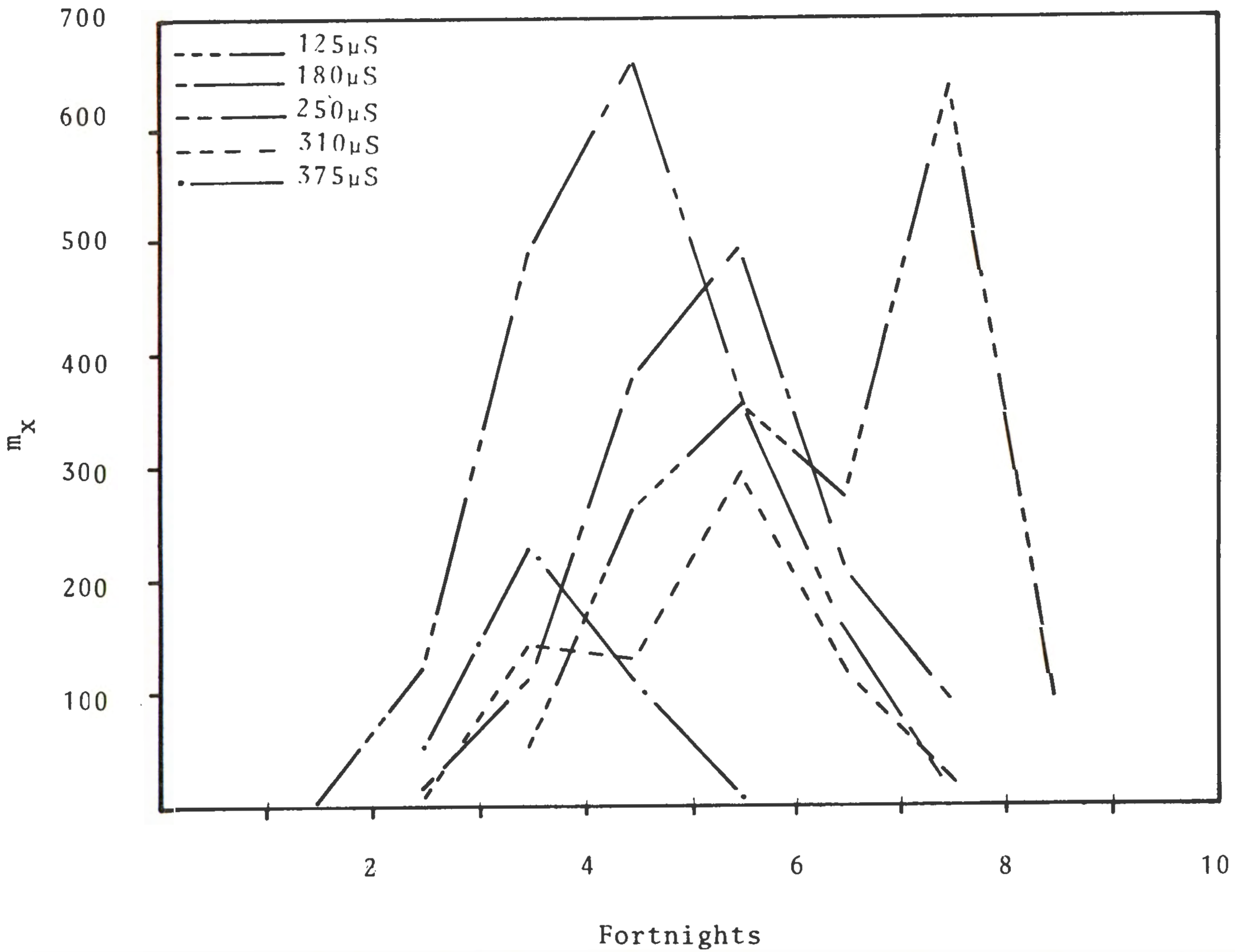


Figure 38. The m_x curves of the cohorts of *L.natalensis* at the various constant conductivities

There is, however, no resemblance between the curves of the cohorts at 310 µS and 375 µS in figures 39 and 40. It has already been mentioned that m_x is the product of the mean number of eggs per egg clutch and the mean number of egg clutches per snail produced per fortnight. According to De Kock (1973), therefore, a resemblance such as exists between the curves in figures 39 and 38 and also between the three curves in figure 40 to those in figures 38 and 39 suggests that, in these particular cases, both the mean number of eggs per egg clutch and the mean number of egg clutches per snail must have influenced the shape of the m_x curves. The lack of resemblance between the curves of the cohorts at 310 µS and 375 µS in figures 39 and 40 indicates that, at these conductivities, the number of eggs per egg clutch contributed more towards the differences in m_x values than did the mean number of egg clutches per snail. In a similar analysis Combrinck (1968) concluded that both these factors influenced the calculation of m_x and therefore the shape of the fecundity curves drawn for *L. natalensis*.

The highest number of egg clutches per snail per fortnight was produced by the cohort at 310 µS (appendix table 19) and the highest number of eggs per egg clutch was recorded for the cohort at 125 µS (appendix table 20). In all the cohorts the number of eggs per egg clutch per fortnight reached a maximum and then declined as the snails approached the end of their reproductive periods (figure 39). This was also the case with the number of egg clutches produced per snail per fortnight (figure 40) with the notable exceptions of the cohorts at 310 µS and 375 µS. Here no peak was reached and the number of egg clutches produced per fortnight steadily increased until the snails stopped depositing eggs.

Since the cohort at 250 µS had a very low mortality rate the V_x curve greatly resembles the m_x curve. This is also true for the cohort at 375 µS (figure 41). In the other cohorts a higher mortality rate occurred much earlier and consequently the V_x and m_x

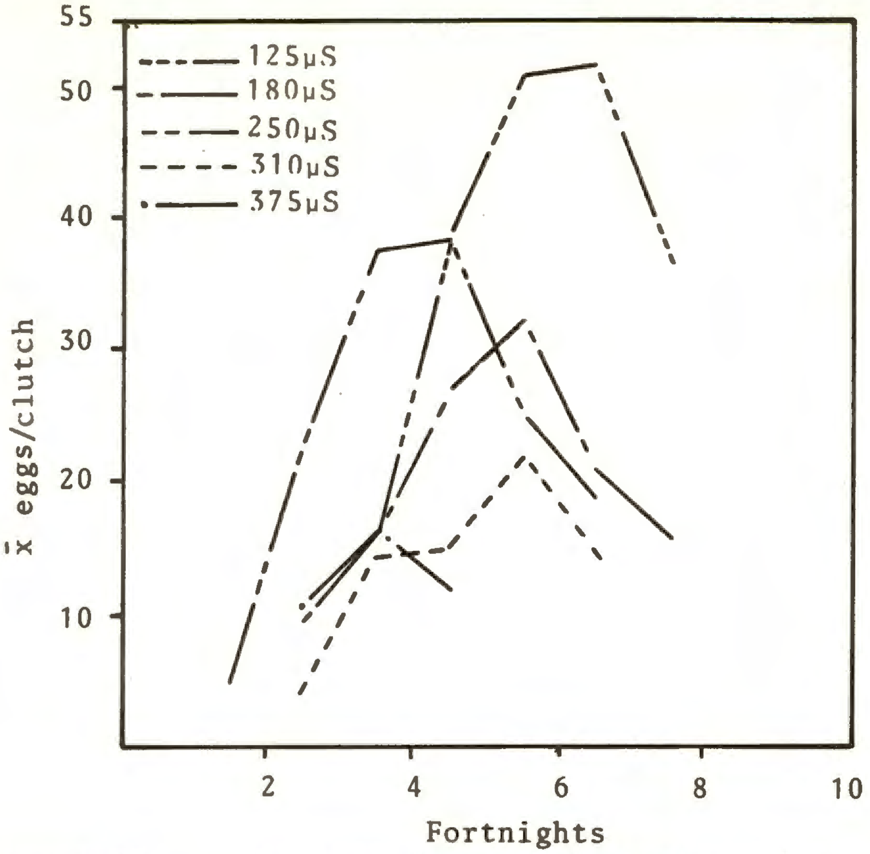


Figure 39. The mean fortnightly number of eggs per egg clutch of *L. natalensis* at the various constant conductivities based on the data contained in Appendix table 20

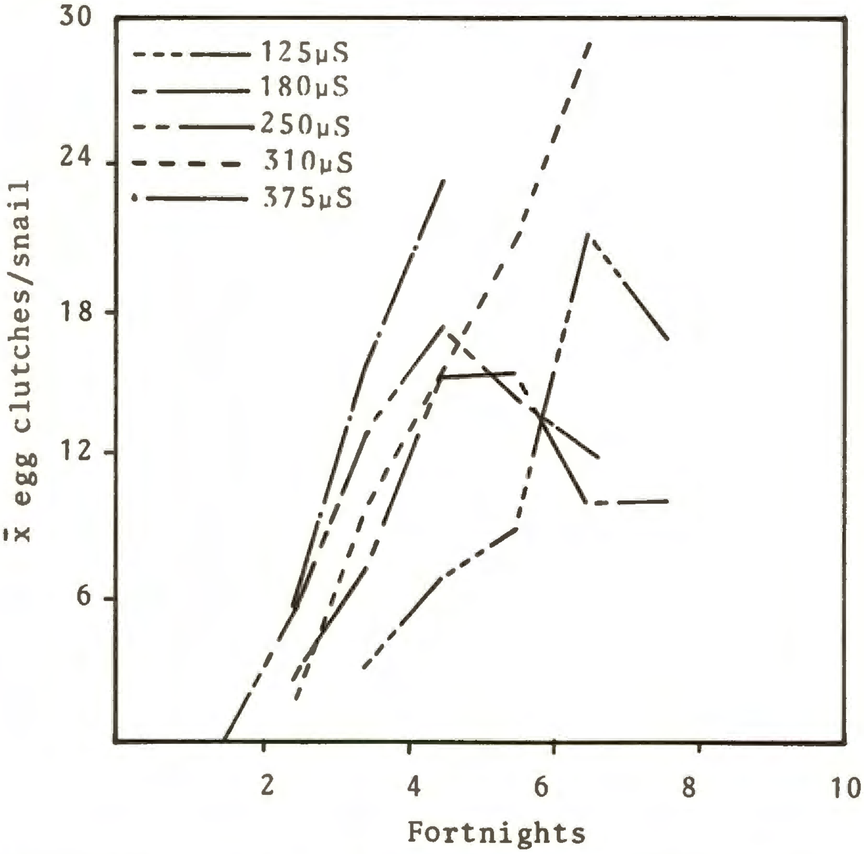


Figure 40. The mean fortnightly number of egg clutches per snail of *L. natalensis* at the various constant conductivities based on the data contained in Appendix table 19

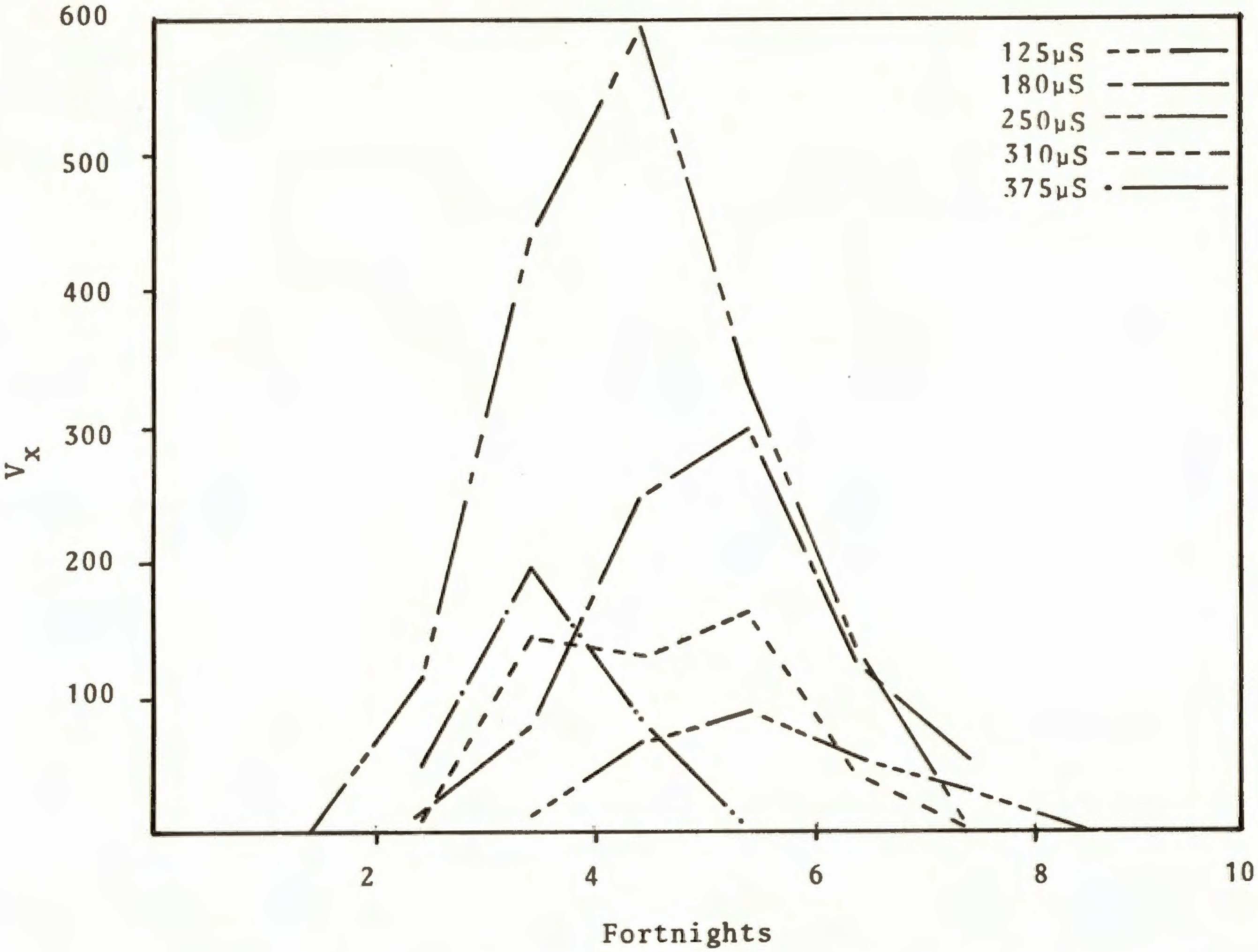


Figure 41. The V_x curves of the cohorts of *L.natalensis* at the various constant conductivities

curves differ from each other considerably. This was responsible for the absence of a second peak in the V_x curve that occurred in the m_x curve of the cohort at 125 µS (figure 38). Likewise the considerable reduction in the height of the peaks in the V_x curves of the cohorts at 180 µS and 310 µS can be attributed to early mortality.

The values of the net reproductive rate (R_o) are presented in table 24 and the increase in the value of R_o per fortnight based on the V_x values in the life tables is graphically presented in figure 42. It is obvious that both the higher and lower conductivities adversely affected the net reproductive rate. The cohorts at 125 µS, 310 µS and 375 µS yielded much lower R_o values than those at 180 µS and 250 µS. The two latter cohorts, moreover, differed considerably as regards their R_o values. From the evidence in figure 42 it seems obvious that the conductivity best suited for *L. natalensis* was 250 µS and it may therefore be assumed that the optimum range for this species, as far as conductivity is concerned, would lie between 180 µS and 310 µS with the actual optimum close to 250 µS.

The success sequence of the cohorts based on the value of T_c was 375 µS < 250 µS < 310 µS < 180 µS < 125 µS. According to this sequence the trend was for T_c to increase in value as conductivities became lower.

Although the most favourable T_c value was achieved at 375 µS, the best survival rates were recorded by the cohorts at 250 µS and 180 µS. The highest m_x, V_x and R_o values were recorded for the cohort at 250 µS. Although the one at 125 µS survived just as long as that at 250 µS, only one specimen survived during the last two fortnights.

Judging from the r_m values calculated for the five cohorts the snails at 250 µS performed best (table 24) with a r_m value of 2,1258. The second best performance was that of the cohort at

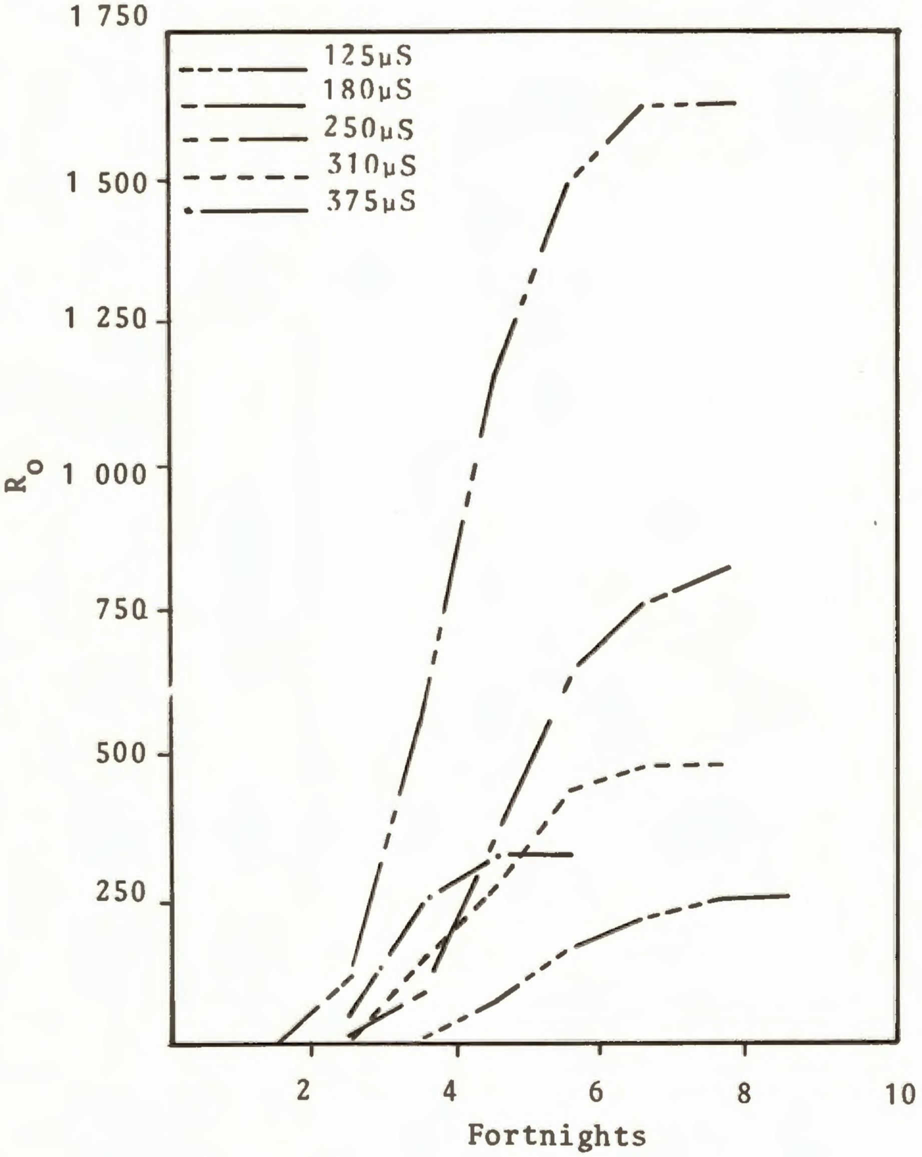


Figure 42. The increase in R_o value per fortnight of the cohorts of *L.natalensis* at the various constant conductivities

375 μS with a r_m value of 1,7791. The difference between the r_m values of the cohorts at 180 μS and 310 μS was 0,0072. According to De Kock (1973) any difference smaller than 0,058 in a cohort of 20 snails cannot be accepted as significant. In this case, therefore, the performance of these two cohorts should be considered as being equal. Consequently the r_m sequence was 250 μS > 375 μS > 180 μS = 310 μS > 125 μS. The high r_m achieved by the cohort at 250 μS could be attributed to a high reproductive rate, high R_o value, the second lowest T_c value and a very short period between hatching and egg production. In spite of having the second highest R_o value the cohort at 180 μS yielded a lower r_m than that at 375 μS because of a much higher T_c value and a lower reproductive rate during those important first reproductive periods.

The similar performance of the cohorts at 180 μS and 310 μS, despite the former having accumulated a R_o value almost twice that of the latter, was the result of higher egg production during the second fortnight, higher survival rates and a better T_c value recorded for the cohort at 310 μS. The factors thus mainly responsible for the particular r_m sequence of *L. natalensis* were m_x and T_c. Survival did not contribute much towards this sequence. Since the r_m values of the cohorts at 125 to 375 μS were all above nil, the finite rate of increase (λ) of all the cohorts had a value of more than one. It consequently follows that a population of *L. natalensis* should be able to increase in numbers at these conductivities.

Although the low salinity at 125 μS inhibited growth in the very young stages, this effect was lost after a while and these snails reached the highest mass recorded for *L. natalensis*. From the statistics in table 24 it can be concluded that the optimum conductivity at which to breed *L. natalensis* lies very close to 250 μS but it is also obvious that none of the conductivity ranges (except for 50 and 500 μS) worked at in this experiment were really unfavourable to this species. The conductivity of 125 μS might be regarded as having been unfavourable to the juvenile stages only.

3.5 Life tables of *B.(B.) tropicus*

180 µS

Fifty five percent of the eggs hatched after six days and egg production commenced 28 days after birth (table 34). Although the snails in this cohort survived for 11 fortnights, mortality already started after the second fortnight (table 25 and figure 43). The fecundity curve (m_x) reached its highest value during the fifth fortnight but as only seven of the original 20 snails were still alive the m_x and V_x curves differ considerably. After this peak the m_x curve dropped sharply with a slight recovery which is also reflected in the V_x curve during the tenth fortnight.

250 µS

Eggs hatched after seven days with a hatching percentage of 70,27% and egg production by the new generation started 20 days later (table 34). Like the cohort at 180 µS these snails survived for 11 fortnights, but egg production ceased after the ninth fortnight (table 26 and figure 44). The m_x curve reached its highest value during the fifth fortnight and in this case the egg curve (V_x) resembles the m_x curve to a great extent. This was due to the very low initial mortality rate which consequently also resulted in much higher V_x values for this cohort than for the previous one. The first mortalities occurred after the fourth fortnight.

310 µS

A hatching percentage of 60,61% was recorded for this cohort. Eggs hatched after seven days and the snails started producing eggs 35 days later (table 34). This was 15 days longer than the

Table 25 : Life table of *B. (B.) tropicus* at 180µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	13	20	1,0000	0,6500	0,6500
2,5	1 018	12	0,6000	84,8333	50,9000
3,5	2 537	7	0,3500	362,4286	126,8500
4,5	2 880	7	0,3500	411,4286	144,0000
5,5	1 574	7	0,3500	224,8571	78,7000
6,5	1 035	6	0,3000	172,5000	51,7500
7,5	392	6	0,3000	65,3333	19,6000
8,5	495	6	0,3000	82,5000	24,7500
9,5	385	3	0,1500	128,3333	19,2500
10,5	64	2	0,1000	32,0000	3,2000

$R_o = \Sigma V_x = 538{,}6500$

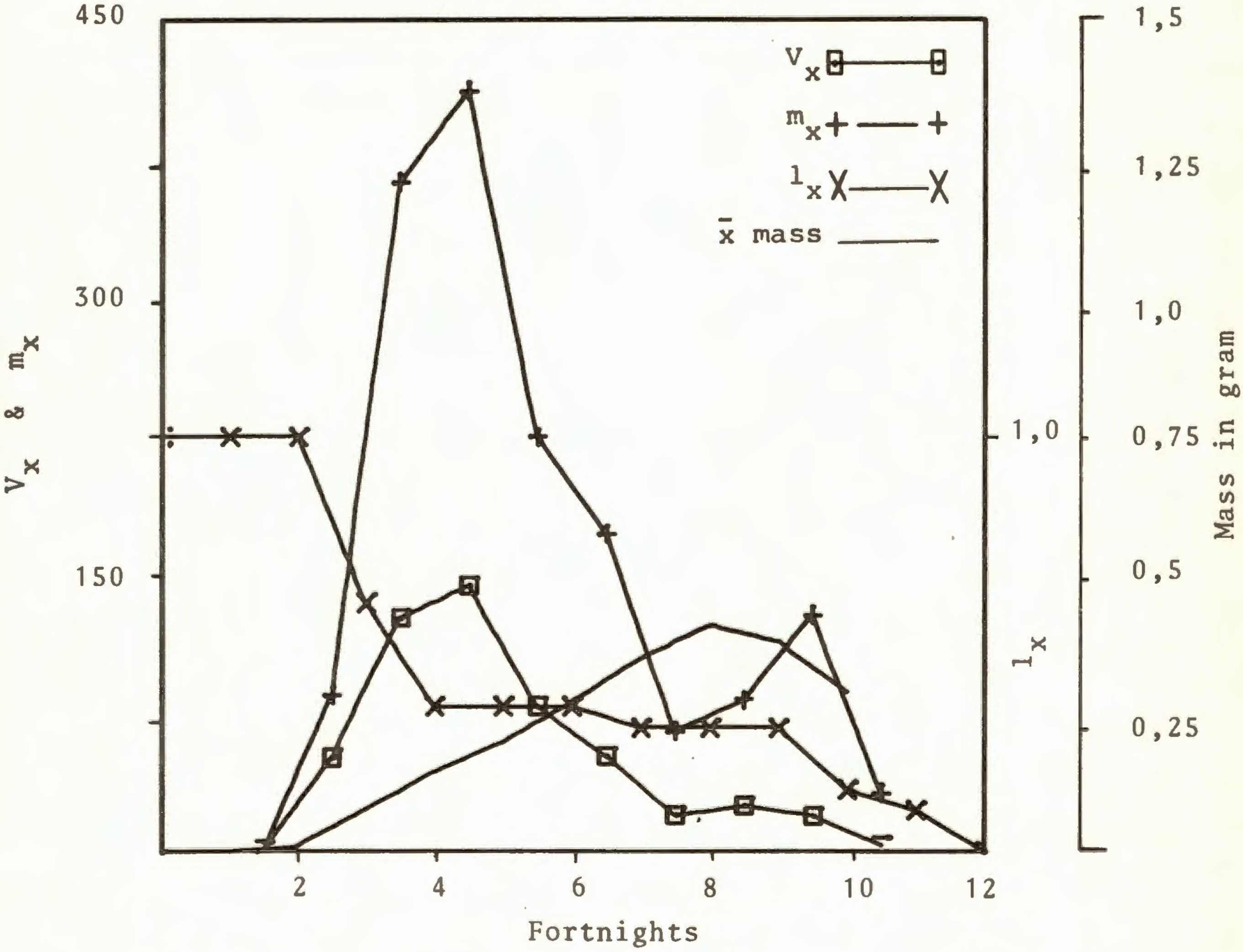


Figure 43. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 180 μS

Table 26 : Life table of *B. (B.) tropicus* at 250µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	1 499	20	1,0000	74,9500	74,9500
2,5	4 540	20	1,0000	227,0000	227,0000
3,5	7 915	20	1,0000	395,7500	395,7500
4,5	7 244	18	0,9000	402,4444	362,2000
5,5	2 862	16	0,8000	178,8750	143,1000
6,5	1 567	13	0,6500	120,5385	78,3500
7,5	271	11	0,5500	24,6364	13,5500
8,5	13	8	0,4000	1,6250	0,6500
9,5	0	5	0,2500	0	0
10,5	0	1	0,0500	0	0

$R_o = \Sigma V_x = 1\ 312{,}5500$

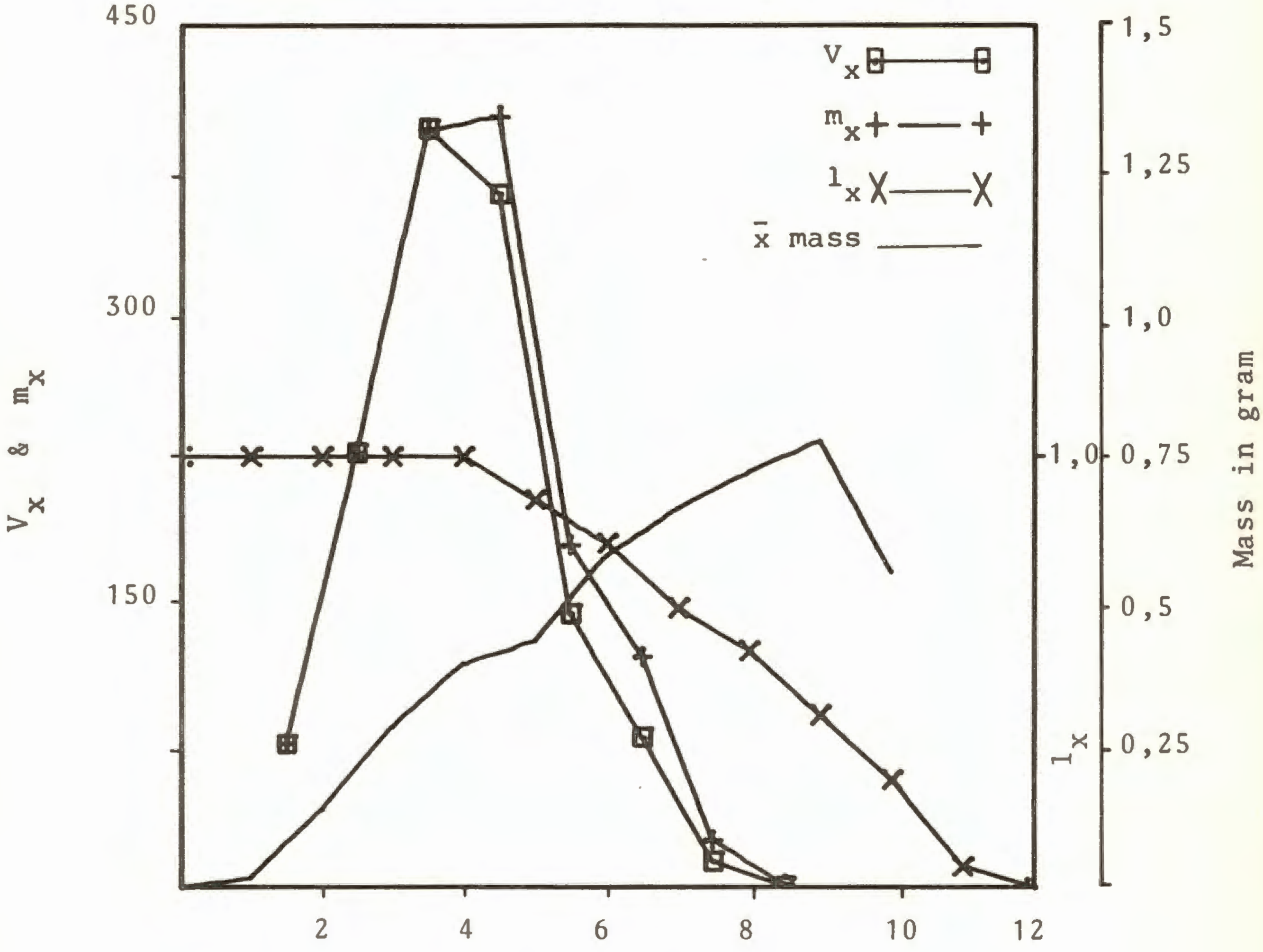


Figure 44. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 250 μS

corresponding period at 250 µS. The m_x and V_x curves differ considerably because during the seventh fortnight, when both reached their highest values, ten of the original 20 snails had already died (table 27 and figure 45). Although the eggs of this cohort hatched within seven days there was an obvious delay in their reaching maturity as is evidenced by the length of the period preceding egg production. Although this delay was also obvious in the cohort of *B. pfeifferi* at the same conductivity (table 18) no significant delay could be discerned in the cohorts of either *B.(P.) globosus* (table 10) or *L. natalensis* (table 24). Whatever factors caused this delay, they apparently only affected *B.(B.) tropicus* and *B. pfeifferi*. The hatching percentages of *B.(B.) tropicus* and *B.(P.) globosus* were, however, similarly affected at this conductivity and both were significantly lower than those of the cohorts immediately above and below them in the conductivity range. The delay in the attainment of maturity was further reflected in the low growth rate of this cohort (figure 45) compared to that of the cohort at 250 µS (figure 44). In spite of the low growth rate, survival was not greatly impaired during the first six weeks after which mortality increased rapidly.

375 µS

Although the eggs hatched within six days the hatching percentage of 66,67% cannot be considered as satisfactory. The period preceding egg production (21 days) was, however, the third shortest recorded for any cohort of *B.(B.) tropicus* (table 34). The lifespan of this cohort, like those of the other species kept at this conductivity, was much shorter than those of these species at other conductivities (table 28 and figure 46). Although this cohort survived for only six fortnights serious mortality did not occur until after the fifth fortnight. Survival was therefore quite satisfactory during those periods so important in the calculation of r_m. The fecundity curve (m_x) reached its highest value, which was very much lower than those of the other cohorts

Table 27 : Life table of *B. (B.) tropicus* at 310µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	652	20	1,0000	32,6000	32,6000
3,5	1 261	20	1,0000	63,0500	63,0500
4,5	1 829	19	0,9500	96,2632	91,4500
5,5	2 887	17	0,8500	169,8235	144,3500
6,5	4 783	10	0,5000	478,3000	239,1500
7,5	1 368	10	0,5000	136,8000	68,4000
8,5	580	6	0,3000	96,6667	29,0000

$R_o = \Sigma V_x = 684{,}0000$

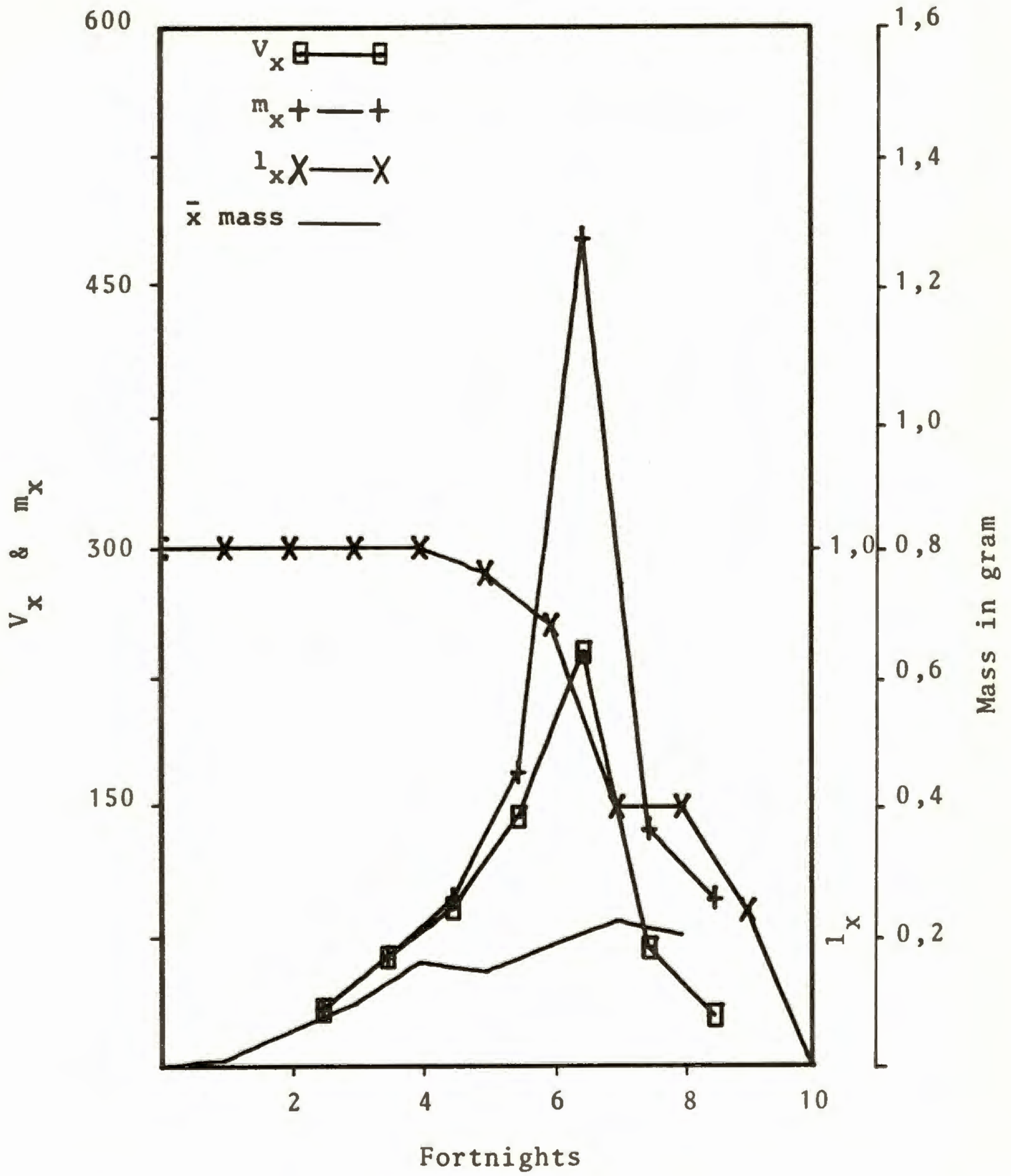


Figure 45. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 310 µS

Table 28 : Life table of *B. (B.) tropicus* at 375µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	509	20	1,0000	25,4500	25,4500
2,5	2 254	20	1,0000	112,7000	112,7000
3,5	4 208	19	0,9500	221,4737	210,4000
4,5	218	17	0,8500	12,8235	10,9000
5,5	0	5	0,2500	0	0

$R_o = \Sigma V_x = 372,4500$

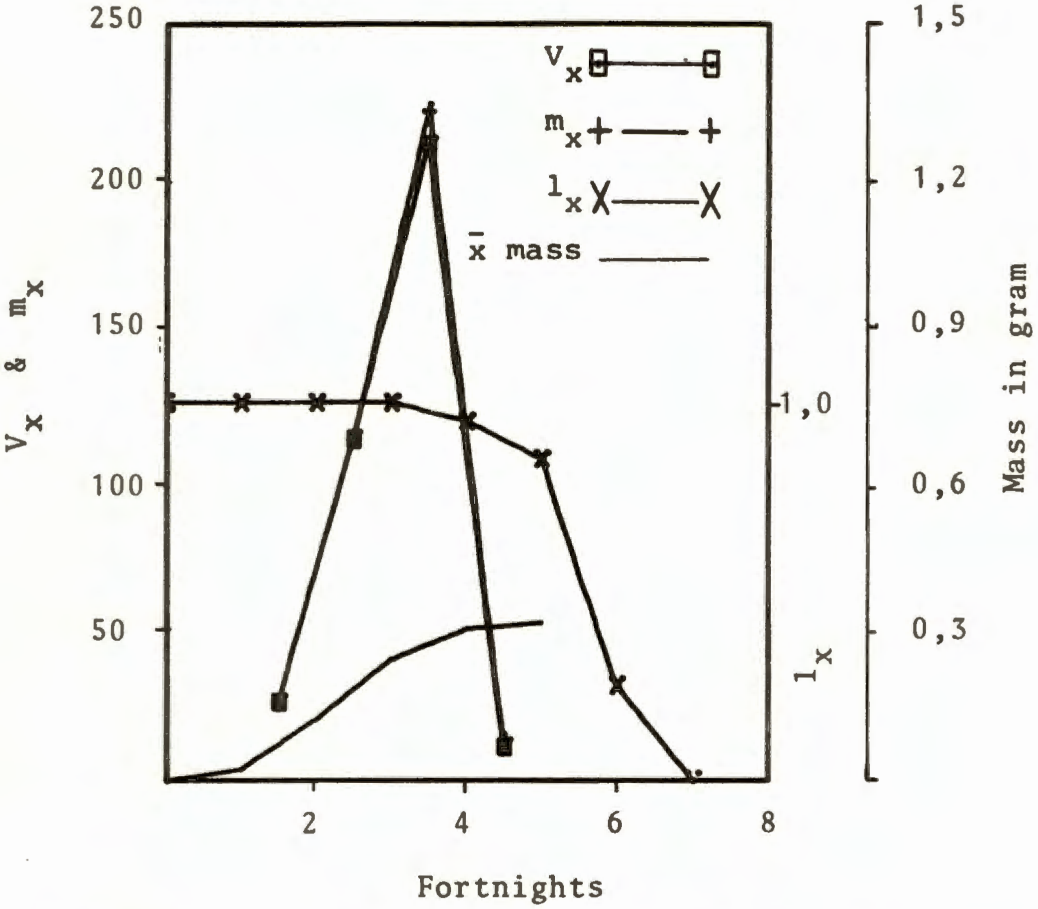


Figure 46. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 375 µS

of *B.(B.) tropicus*, during the fourth fortnight at which time only one snail had died. Consequently the m_x and V_x curves are prac=tically identical. During the sixth fortnight, when five snails were still alive, no eggs were produced. The egg production of this cohort for the first two fortnights which contributes so much to the eventual value of r_m was surpassed only by the co=horts at 250 μS, 625 μS and 750 μS.

500 μS

The hatching time of this cohort was seven days and 78,94% of the eggs hatched. Egg production started 28 days after hatching. This was the same as for the cohort at 180 μS but longer than for the cohorts at 250 μS, 375 μS, 625 μS and 750 μS (table 34). The snails survived for ten fortnights and the first mortality occurred after the fourth fortnight. The fecundity curve reached its highest peak during the seventh fortnight but due to the fact that this was reached after the onset of mortalities the m_x and V_x curves differ considerably from each other (table 29 and figure 47).

625 μS

Although the eggs of this cohort took two days longer to hatch than those of the cohorts closest to it in the conductivity range (table 34) the hatching percentage of 92,59% was second highest for *B.(B.) tropicus*. Egg production started 20 days after the snails had hatched. The highest m_x value was recorded during the sixth fortnight but due to the effect of mortalities which set in after the second fortnight the highest V_x value was reached during the fourth fortnight. Consequently there is no resemblance between the m_x and V_x curves (table 30 and figure 48). As a re=sult of six m_x values higher than 400, of which four were higher than 500, the m_x curve shows no sharp peak. The snails in this cohort maintained a very high reproductive rate especially during the first three fortnights. The cohort survived for 11 fort=nights and mortalities commenced after the second fortnight.

Table 29 : Life table of *B. (B.) tropicus* at 500µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	87	20	1,0000	4,3500	4,3500
2,5	560	20	1,0000	28,0000	28,0000
3,5	810	20	1,0000	40,5000	40,5000
4,5	1 880	19	0,9500	98,9474	94,0000
5,5	2 562	16	0,8000	160,0625	128,0500
6,5	5 662	14	0,7000	404,4286	283,1000
7,5	3 863	12	0,6000	321,9167	193,1500
8,5	584	7	0,3500	83,4286	29,2000
9,5	12	3	0,1500	4,0000	0,6000

$R_o = \Sigma V_x = 818{,}9500$

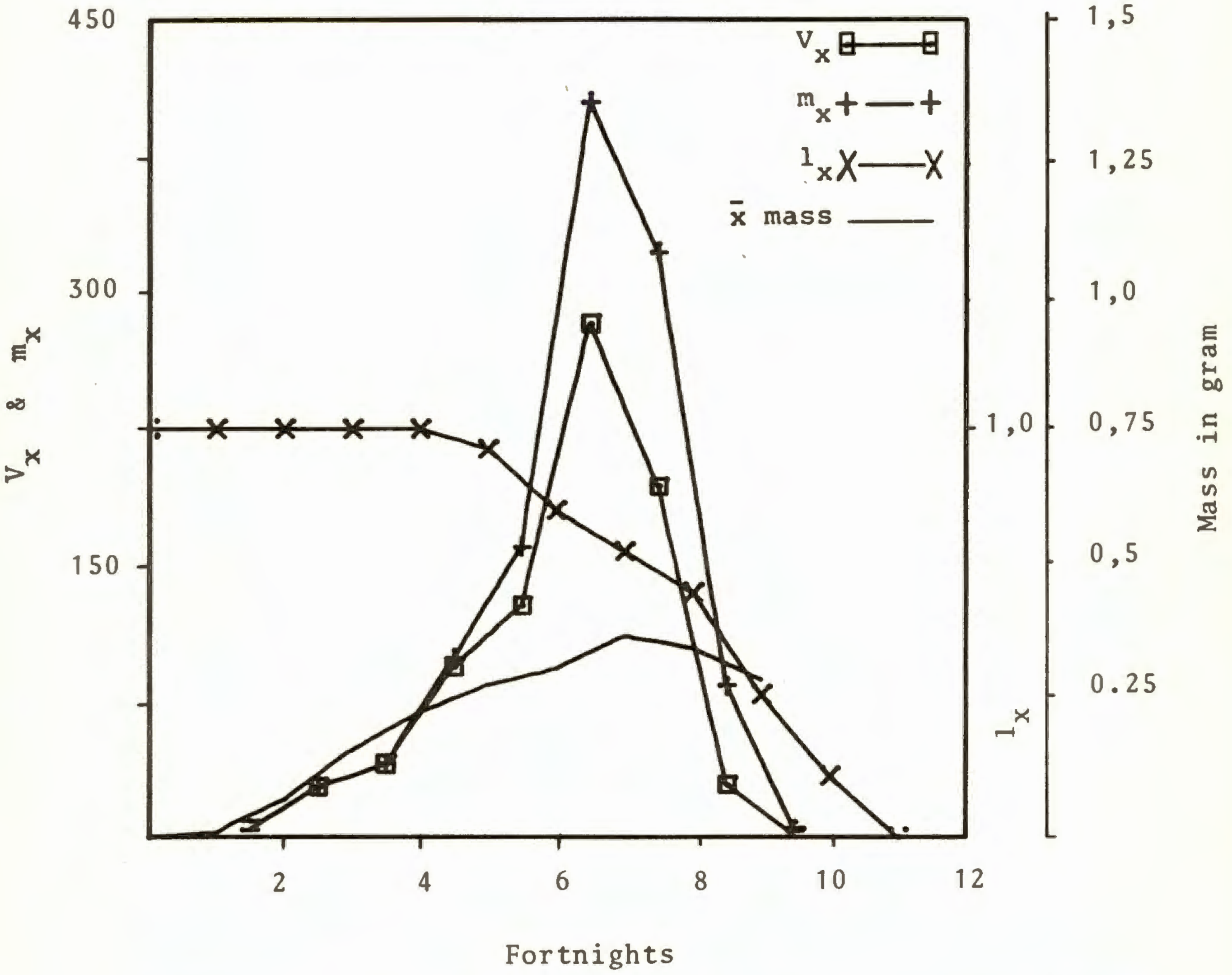


Figure 47. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 500 µS

Table 30 : Life table of *B. (B.) tropicus* at 625µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	2 108	20	1,0000	105,4000	105,4000
2,5	7 888	19	0,9500	415,1579	394,4000
3,5	9 301	17	0,8500	547,1176	465,0500
4,5	7 851	14	0,7000	560,7857	392,5500
5,5	7 261	12	0,6000	605,0833	363,0500
6,5	5 591	10	0,5000	559,1000	279,5500
7,5	4 304	9	0,4500	478,2222	215,2000
8,5	2 343	9	0,4500	260,3333	117,1500
9,5	553	7	0,3500	79,0000	27,6500
10,5	0	3	0,1500	0	0

$R_o = \Sigma V_x = 2\ 378{,}0000$

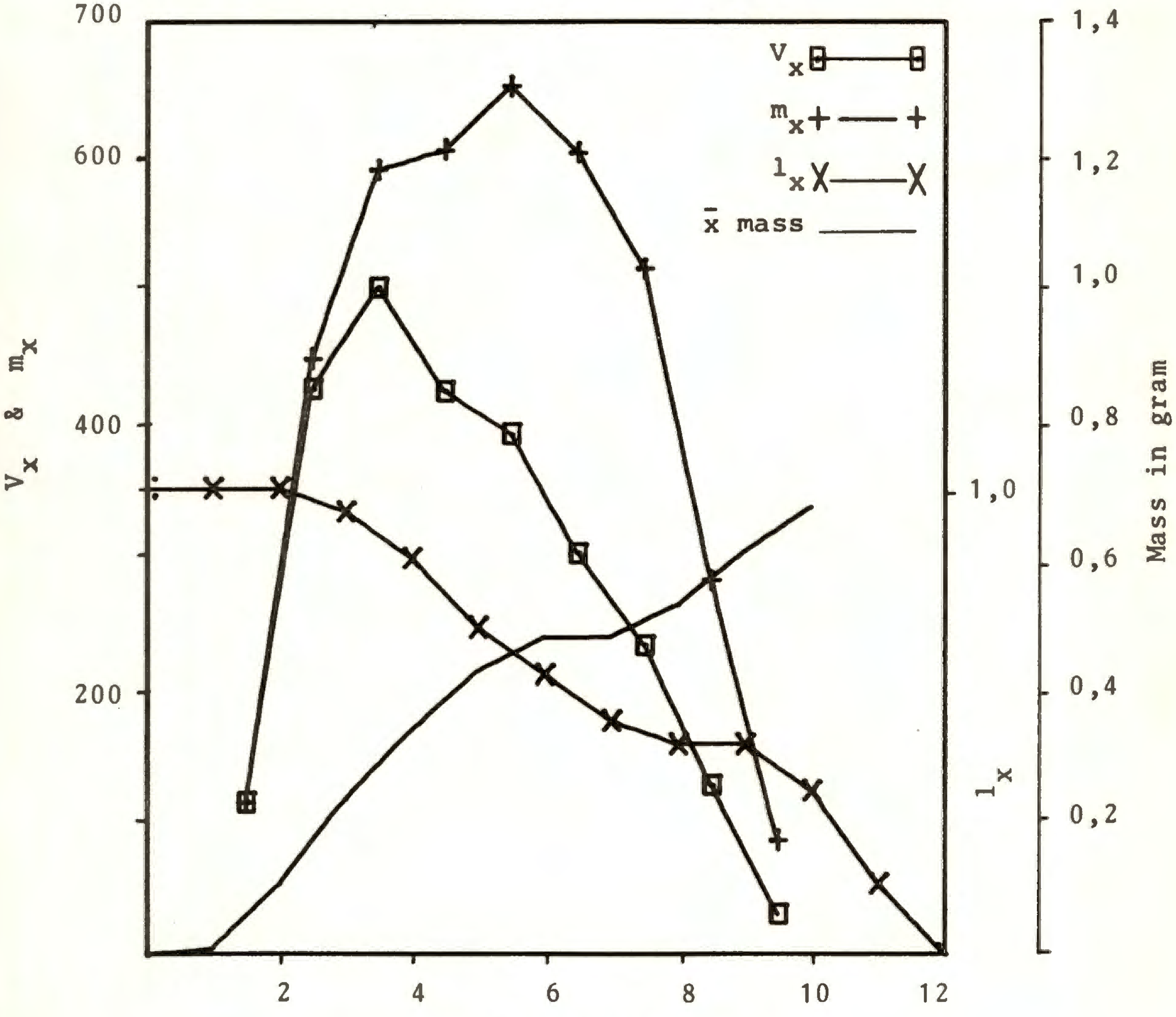


Figure 48. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 625 μS

No eggs were produced during the last fortnight.

750 µS

Eggs at this conductivity hatched in seven days and the highest hatching percentage for *B.(B.) tropicus* (93,06%) was recorded here (table 34). This cohort had the shortest pre-egg laying period (19 days). Mortalities started after the third fortnight and after the fifth fortnight more than half of the original snails had died (table 31 and figure 49). Although this cohort yielded the higest m_x value recorded for *B.(B.) tropicus* during this experiment, its highest V_x value was only third highest. This was due to the high mortality rate after the fourth fortnight. As a result of this there is no similarity between the V_x- and m_x curves and from table 31 it can be seen that although the highest V_x value was recorded during the fourth fortnight the highest m_x value only occurred three fortnights later. No eggs were produced during the last two fortnights and despite the high mortality rates this cohort survived longer (14 fortnights) than any cohorts of *B.(B.) tropicus*.

875 µS

Although 90,57% of the eggs at this conductivity hatched within seven days, which compared favourably with the best performances of the other cohorts, the period of 37 days between hatching and first egg production was the longest for any cohort of *B.(B.) tropicus* (table 34). Mortalities occurred after the first fortnight and the rate was especially high after the first and again after the sixth fortnight (table 32 and figure 50). This, coupled with the low reproductive rate during the first two reproductive fortnignts and the long period preceding egg production, had an adverse effect on the eventual value of r_m. As a result of fluctuating egg production the m_x curve shows three peaks, the highest of which coincides with the tenth fortnight. Due to the early high mortality rate the m_x and V_x curves show no resemblance to each other and this was also the reason for

Table 31 : Life table of *B. (B.) tropicus* at 750µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	988	20	1,0000	49,4000	49,4000
2,5	5 811	20	1,0000	290,5500	290,5500
3,5	6 617	17	0,8500	389,2353	330,8500
4,5	5 537	11	0,5500	503,3636	276,8500
5,5	4 296	7	0,3500	613,7143	214,8000
6,5	3 890	5	0,2500	778,0000	194,5000
7,5	1 945	5	0,1500	389,0000	58,3500
8,5	1 495	3	0,1500	498,3333	74,7500
9,5	984	3	0,1500	328,0000	49,2000
10,5	638	3	0,1500	212,6667	31,9000
11,5	264	3	0,1500	88,0000	13,2000
12,5	0	2	0,1000	0	0
13,5	0	2	0,1000	0	0

$R_o = \Sigma V_x = 1\ 604{,}3500$

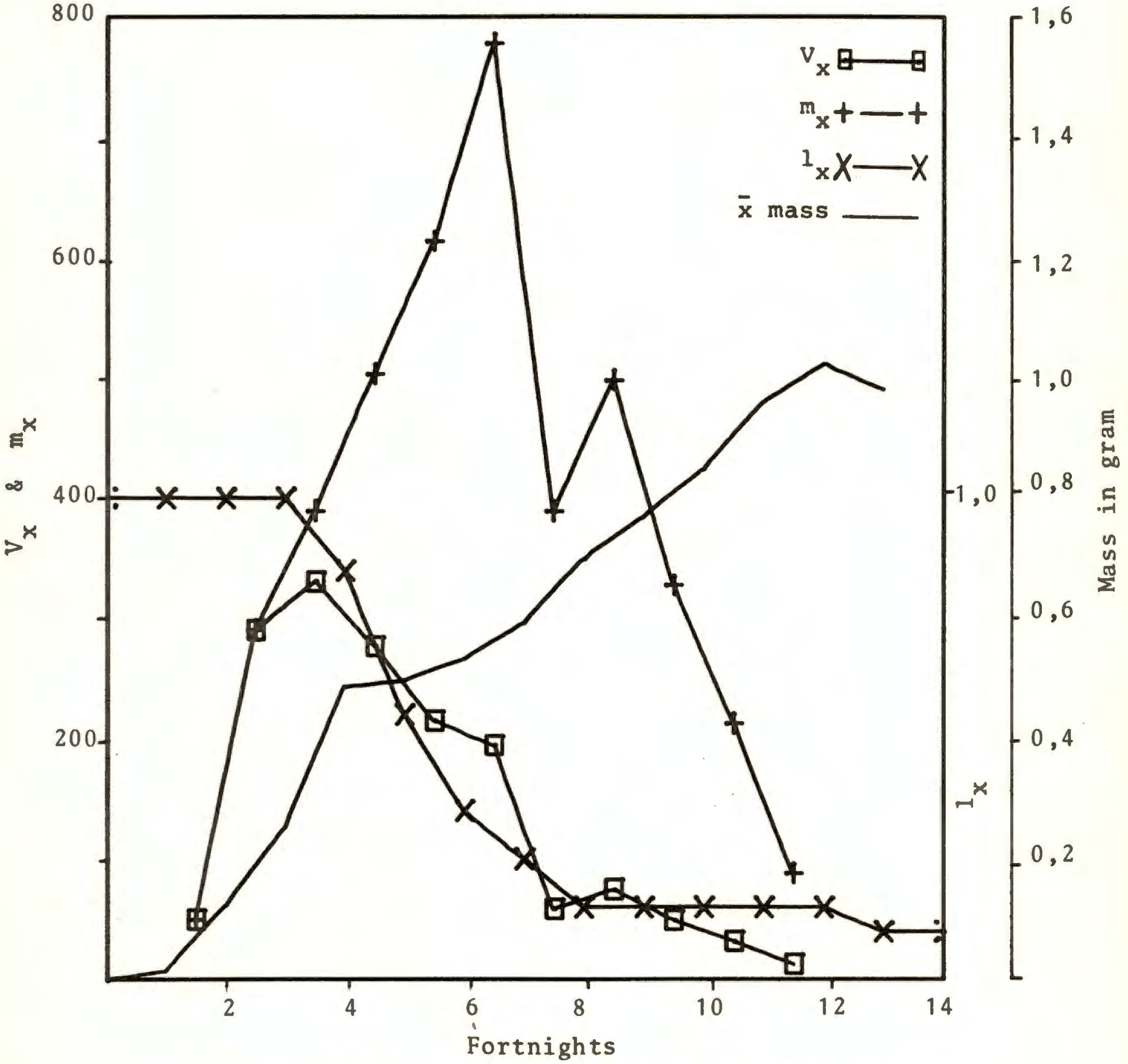


Figure 49. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 750 µS

Table 32 : Life table of *B. (B.) tropicus* at 875μS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	14	0,7000	0	0
2,5	321	14	0,7000	22,9268	16,0488
3,5	2 039	13	0,6500	156,8462	101,9500
4,5	3 486	13	0,6500	268,1538	174,3000
5,5	1 277	13	0,6500	98,2308	63,8500
6,5	2 122	6	0,3000	353,6667	106,1000
7,5	1 159	6	0,3000	193,1667	57,9500
8,5	2 820	6	0,3000	470,0000	141,0000
9,5	2 022	4	0,2000	505,5000	101,1000
10,5	104	2	0,1000	52,0000	5,2000

$R_o = \Sigma V_x = 785,4988$

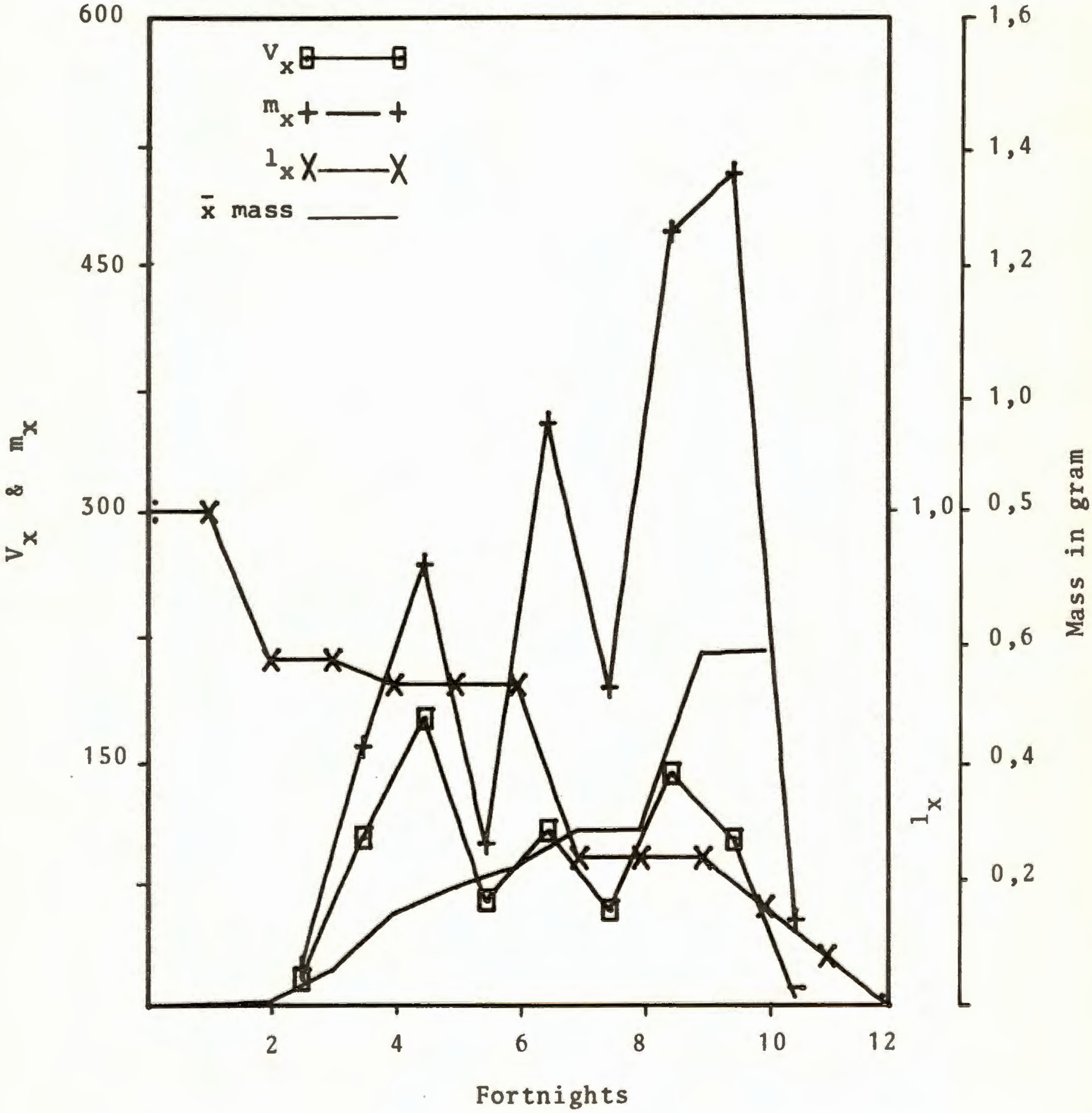


Figure 50. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 875 µS

the big differences between their corresponding values.

1000 µS

The eggs at this conductivity took the same time to hatch as the eggs at 875 µS, i.e. seven days. The hatching percentage of 75,76% was, however, lower than that of the latter. Eggs were produced 35 days after hatching and a much higher egg production was maintained at 1000 µS than at 875 µS.(table 34). The fecun= dity curve reached its peak during the fifth fortnight and this was the second highest m_x value recorded by this species (table 33 and figure 51). The highest V_x value was also recorded during the fifth fortnight but as only 11 snails still survived at that time the m_x and V_x curves differ considerably. The cohort survived for 11 fortnights but no eggs were produced during the last fortnight.

Analysis

At 125 µS the eggs of *B.(B.) tropicus* took nine days to hatch but the hatchlings were unable to survive at this low conductivi= ty (table 34). There was very little difference between the hatching times of the cohorts at the other conductivities. The only exception was the one at 625 µS where hatching time was nine days. As this was two days longer than that of the eggs at both 500 µS and 750 µS it can reasonably be assumed that seven days would also be the hatching time at 625 µS and that the two day delay was exceptional. The shortest hatching time of six days was recorded at 180 µS and 375 µS and it would appear that conductivities above 180 µS has no effect on hatching time.

The highest hatching percentage was recorded at 750 µS with that at 625 µS only slightly lower. From the data in table 34 it seems as if the hatching percentage increased with increasing conductivities up to a value somewhere between 625 µS and 750 µS. At conductivities above 875 µS the hatching percentages dropped notably.

Table 33 : Life table of *B. (B.) tropicus* at 1 000µS.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	12	0,6000	0	0
2,5	657	12	0,6000	54,7500	32,8500
3,5	7 012	11	0,5500	637,4545	350,6000
4,5	8 123	11	0,5500	738,4545	406,1500
5,5	6 650	11	0,5500	604,5455	332,5000
6,5	5 568	9	0,4500	618,6667	278,4000
7,5	3 243	9	0,4500	360,3333	162,1500
8,5	265	7	0,3500	37,8571	13,2500
9,5	98	6	0,3000	16,3333	4,9000
10,5	0	6	0,3000	0	0

$R_o = \Sigma V_x = 1\ 597{,}8000$

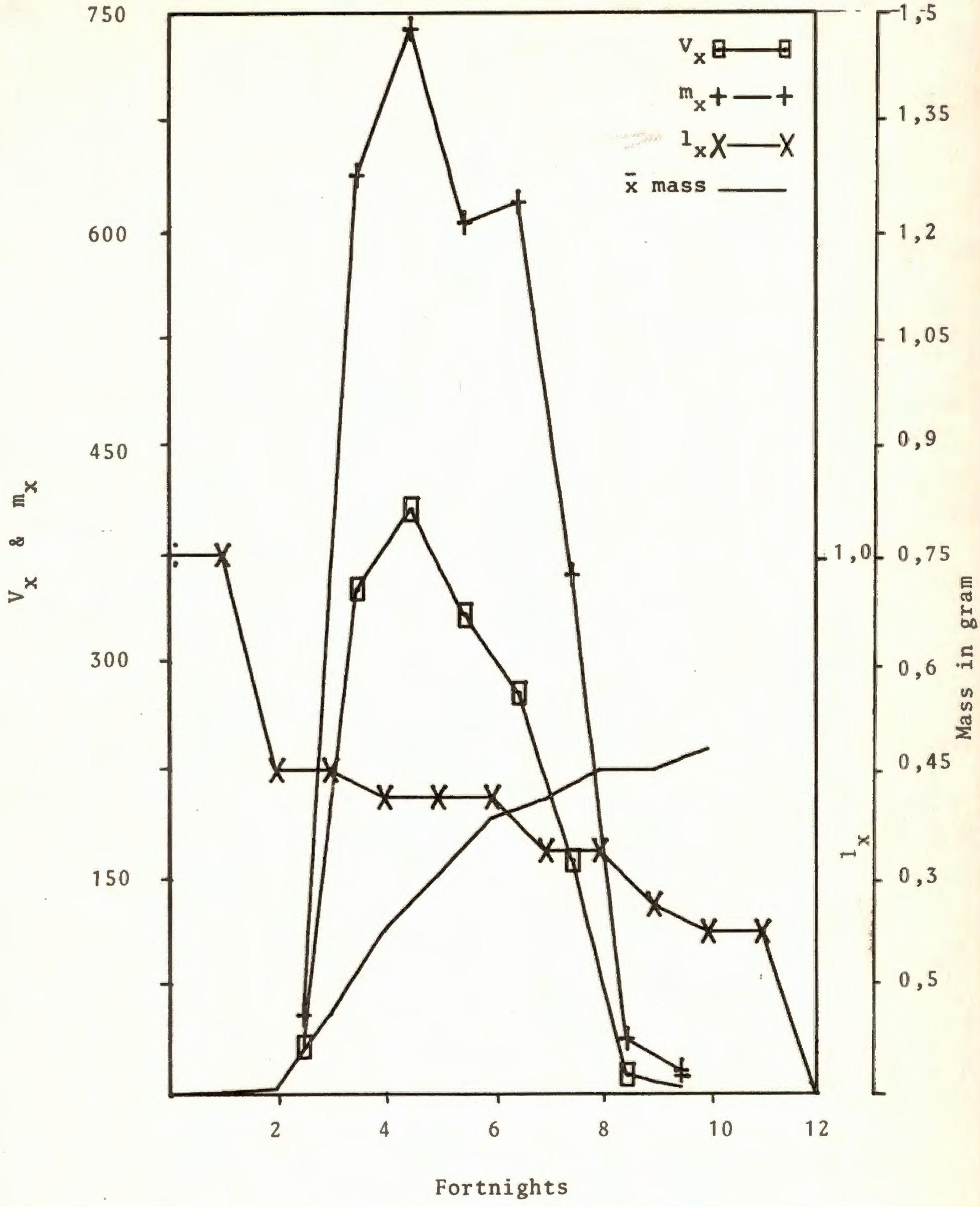


Figure 51. V_x, m_x, l_x values and mean fortnightly mass per snail of the cohort of *B.(B.)tropicus* at a conductivity of 1 000 µS

Table 34 : Population statistics of cohorts of *B.(B.)tropicus*.

Conductivity	Hatching time*	Hatching percentage	Start of egg pro= duction*	λ	r_m	r_c	R_o	T_c
50 µS	-	0	-	-	-	-	-	-
125 µS	9	13,09	-	-	-	-	-	-
180 µS	6	55,05	28	5,807	1,7590	1,218	538,65	5,164
250 µS	7	70,27	20	19,714	2,9813	1,792	1 312,55	4,007
310 µS	7	60,61	35	4,832	1,5752	1,124	684,00	5,809
375 µS	6	66,67	21	11,154	2,4121	1,874	372,45	3,160
500 µS	7	78,94	28	5,254	1,6590	1,082	818,95	6,200
625 µS	9	92,59	20	24,627	3,2038	1,620	2 378,00	4,800
750 µS	7	93,06	19	16,673	2,8138	1,494	1 604,35	4,941
875 µS	7	90,57	37	4,659	1,5389	1,031	785,49	6,464
1 000 µS	7	75,76	35	6,312	1,8425	1,415	1 597,80	5,213

*In days
r_m-range = 1,6649

The period between hatching and the onset of egg production was shortest at 750 µS, the conductivity at which the highest hatching percentage was recorded. Between 250 µS and 750 µS this period remained practically unchanged, except for the values obtained at 310 µS and 500 µS which were 35 and 29 days respectively instead of the expected 20 days. At these two conductivities the reaching of maturity must, therefore, have been delayed by some unknown factor(-s). At conductivities higher than 750 µS the maturation periods were much more extended, possibly as a result of the very low growth rate of these snails (appendix table 10). This also applied to the conductivity of 180 µS where the period was 28 days.

All the foregoing facts point to 750 µS, or thereabouts, as being the most favourable conductivity at which to breed *B.(B.) tropicus*.

No obvious relationship could be demonstrated between salinity and growth within the conductivity ranges evaluated in this experiment. From the data in appendix table 21 and also the curves in figure 52 it appears that the cohort at 250 µS enjoyed a small advantage and was only temporarily overtaken during fortnights four and five by the cohort at 750 µS. Although the latter cohort eventually attained the highest mean mass per snail this could greatly be attributed to its longer survival. The cohort at 625 µS achieved the third highest growth rate and mean mass although its growth rate was lower than that of the cohort at 375 µS during the first three fortnights. The lowest growth rate was recorded at 310 µS. This resulted in a very long maturation period and a consequent first egg production 35 days after hatching. The cohort at 875 µS grew slowly during the first four fortnights but it then overtook the one at 310 µS. The sudden sharp increase in the mean individual mass displayed by the curve of the cohort at 875 µS was caused by the death of a few relatively small specimens. This will illustrate how the loss of certain specimens may influence the mean mass calculated. Ideally, therefore, mean masses should,

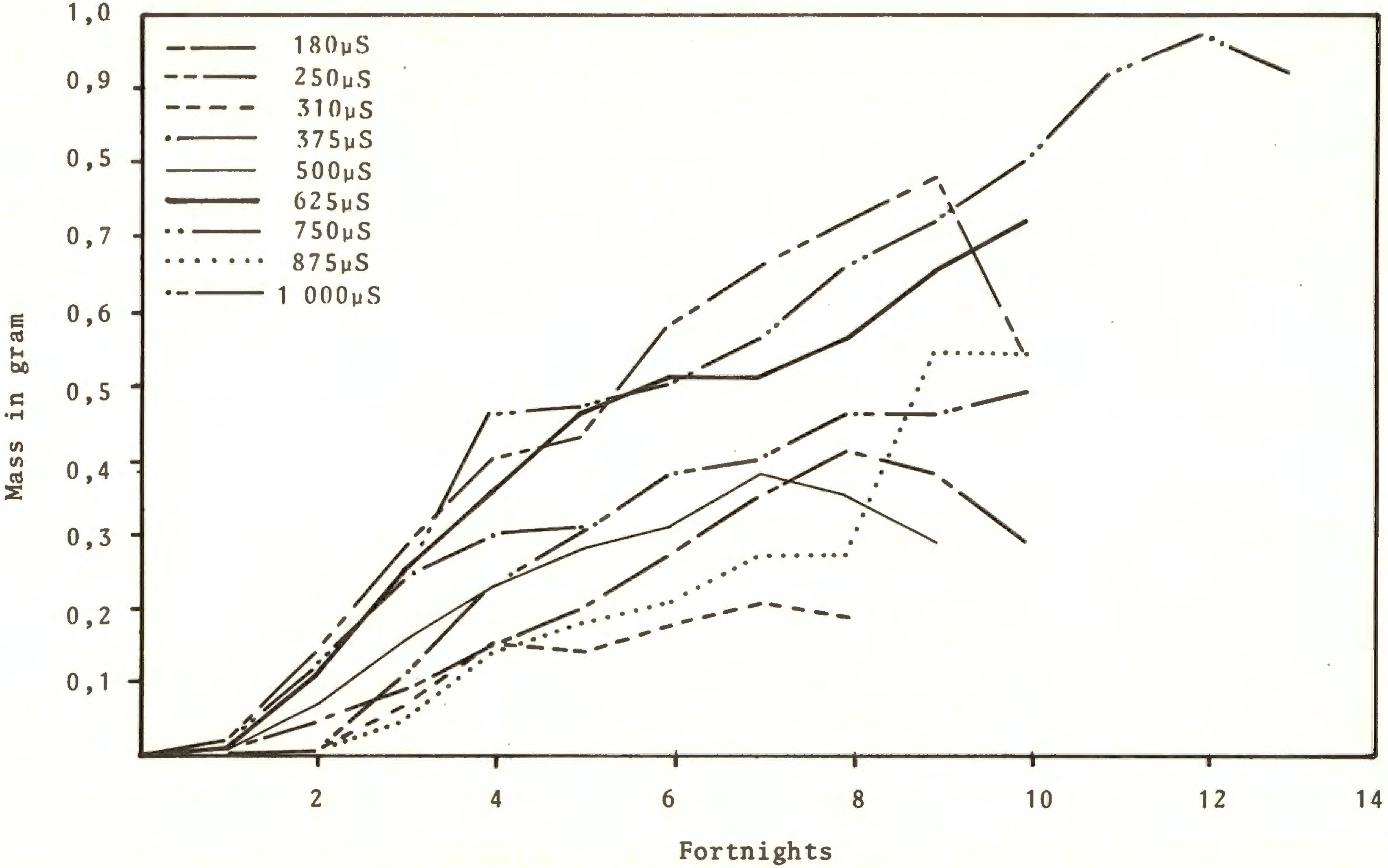


Figure 52. Mean fortnightly mass per snail of the cohorts of *B.(B.)tropicus* at the various constant conductivities based on the data contained in Appendix table 21

wherever possible, be compared before the onset of mortality. This, unfortunately, is very often ruled out by very early mortalities. A very strong relationship was borne out between growth rate and the length of the period between hatching and first egg production. The cohorts at 180 µS, 310 µS, 500 µS, 875 µS and 1000 µS in which the periods preceding egg production was longest also yielded the lowest growth rates.

An examination of the 1_x curves in figure 53 reveals high mortalities during the first four fortnights at both the very high and very low conductivities. This emphasizes the vulnerability, at least during the first four fortnights, of the young snails when subjected to the extremes in any set of conditions. Once the survivors had reached a certain viability, however, their growth and reproduction rates were unaffected and in certain cases their performances were even much better than those of cohorts with low mortalities during the first four fortnights such as those at 625 µS and 750 µS (table 34 and figure 52). The longest surviving cohort was the one at 750 µS while the one at 1000 µS also showed excellent survivorship and longevity.

The m_x sequence of the different cohorts on the basis of the highest values calculated for them, was: 750 µS > 1000 µS > 625 µS > 875 µS > 310 µS > 180 µS > 500 µS > 250 µS > 375 µS.

This suggests that, by and large, the highest m_x values were calculated for the cohorts at the higher salinities. The highest values for the respective cohorts, were, however, not necessarily obtained for the same fortnight (see the tables).

The remarkable similarity between the curves in figure 54 and those in figure 55 indicates that the mean numbers of egg clutches produced per snail per fortnight contributed more towards the corresponding m_x values than did the mean number of eggs per egg clutch per fortnight which are graphically presented in figure 56. The resemblance between the curves in figures

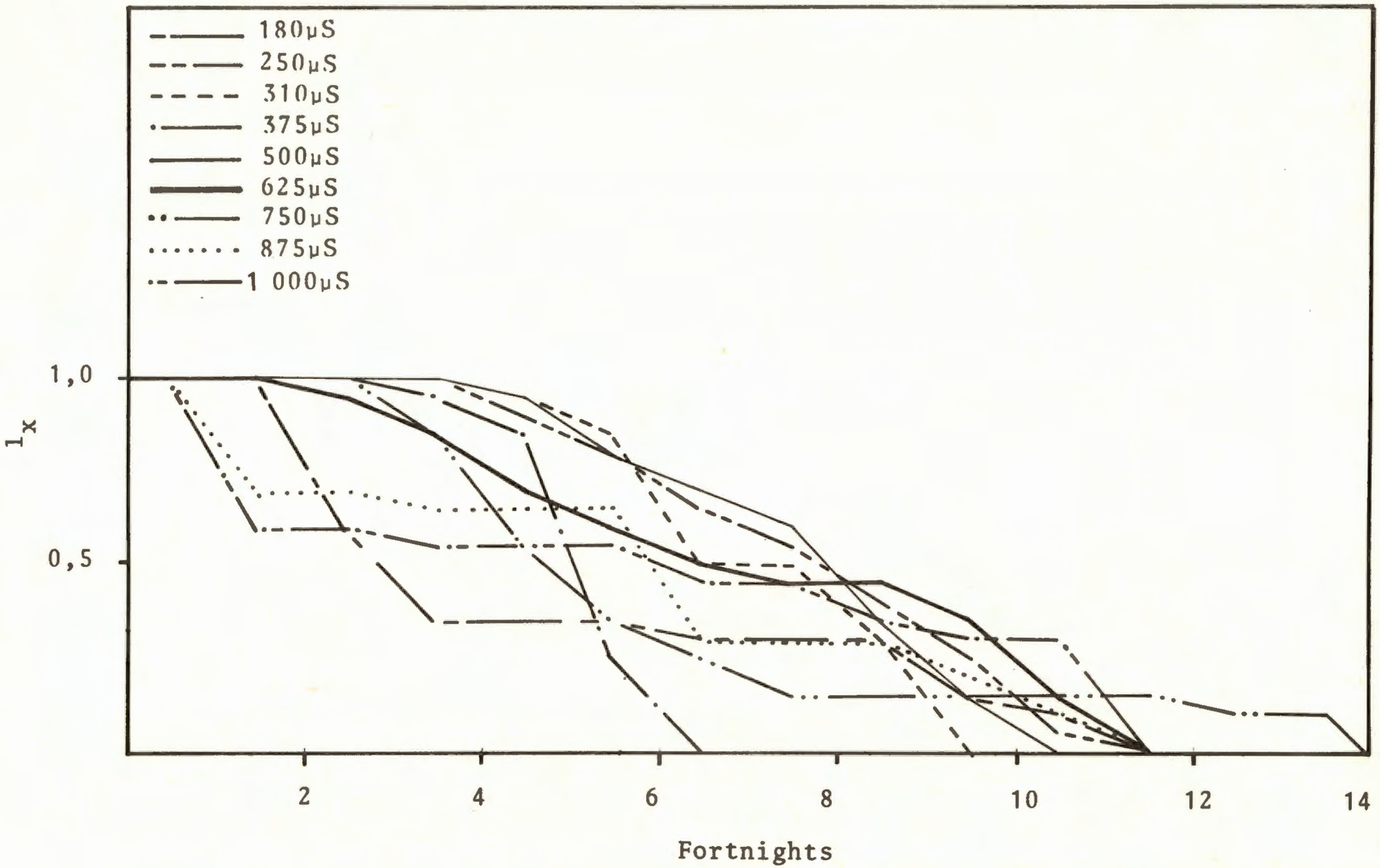


Figure 53. The 1_x curves of the cohorts of *B.(B.)tropicus* at the various constant conductivities

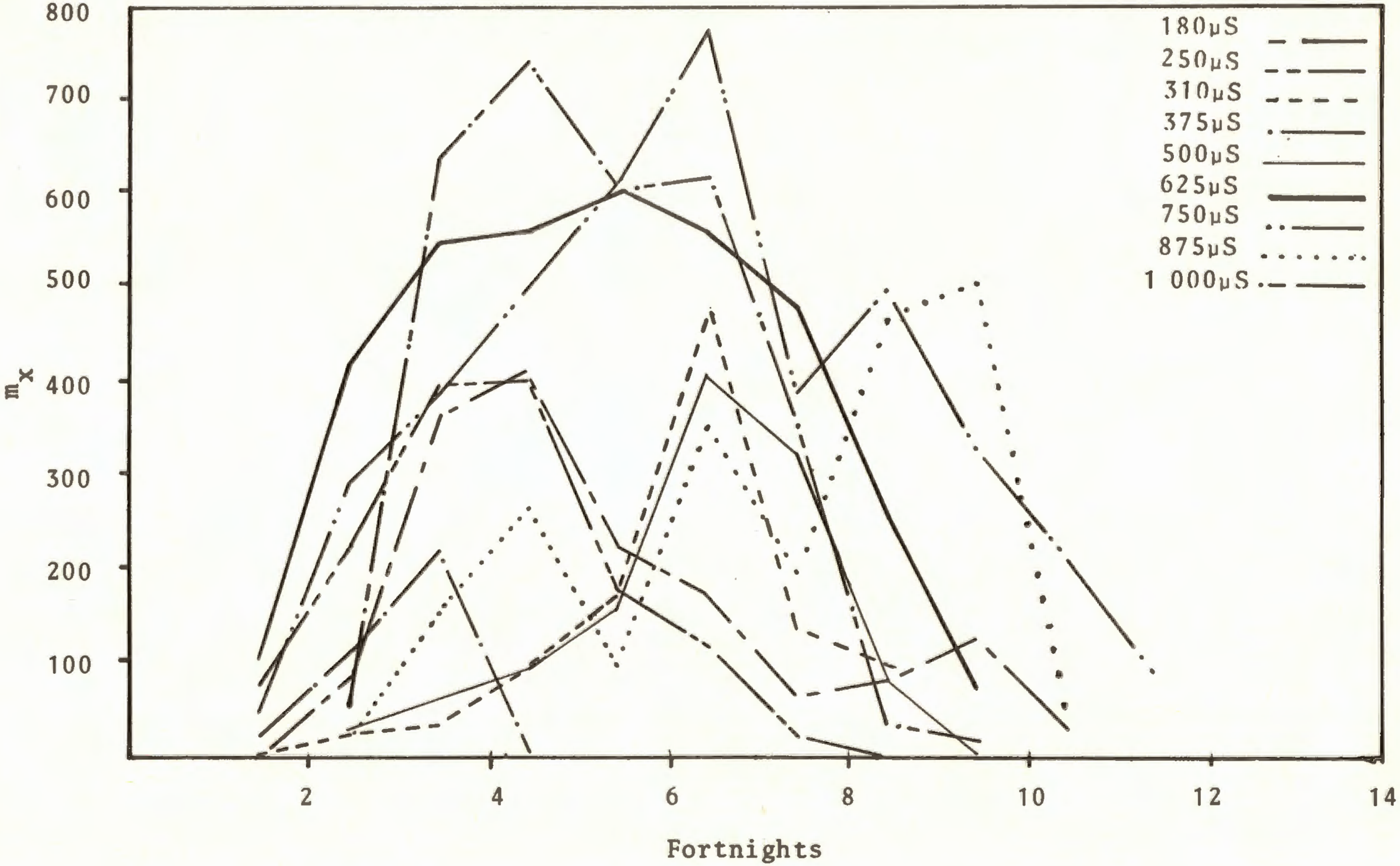


Figure 54. The m_x curves of the cohorts of *B.(B.)tropicus* at the various constant conductivities

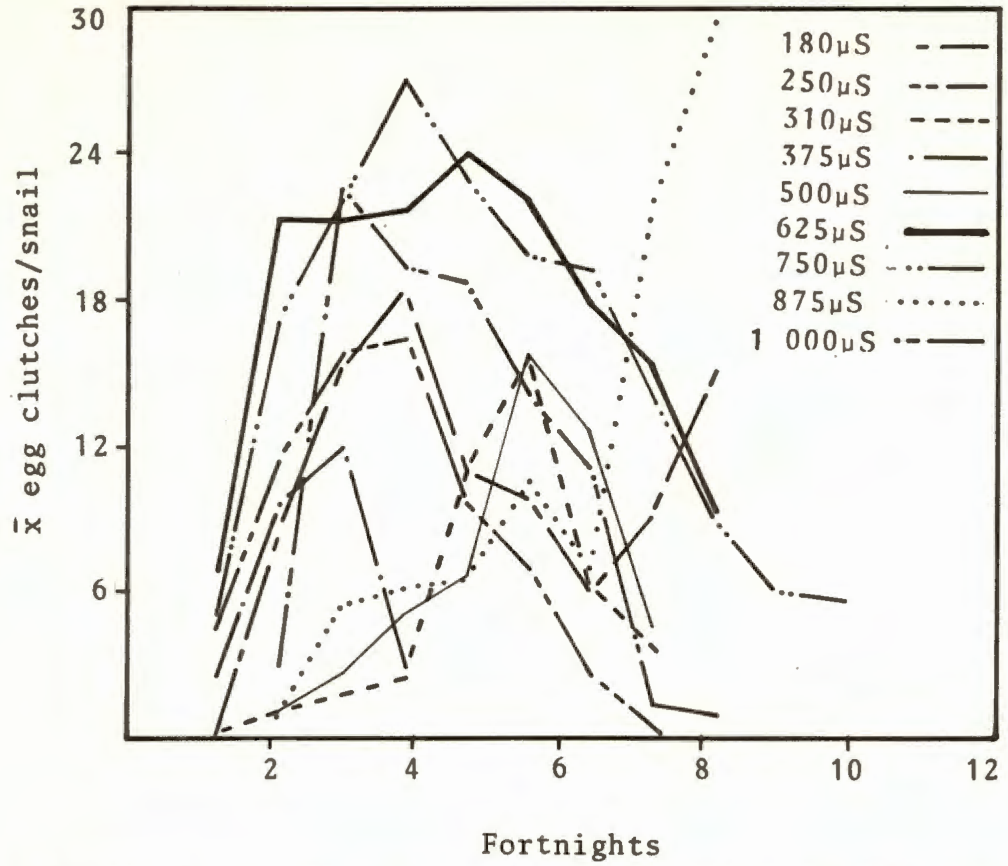


Figure 55. The mean fortnightly number of egg clutches per snail of *B.(B.) tropicus* at the various constant conductivities based on the data contained in Appnedix table 22

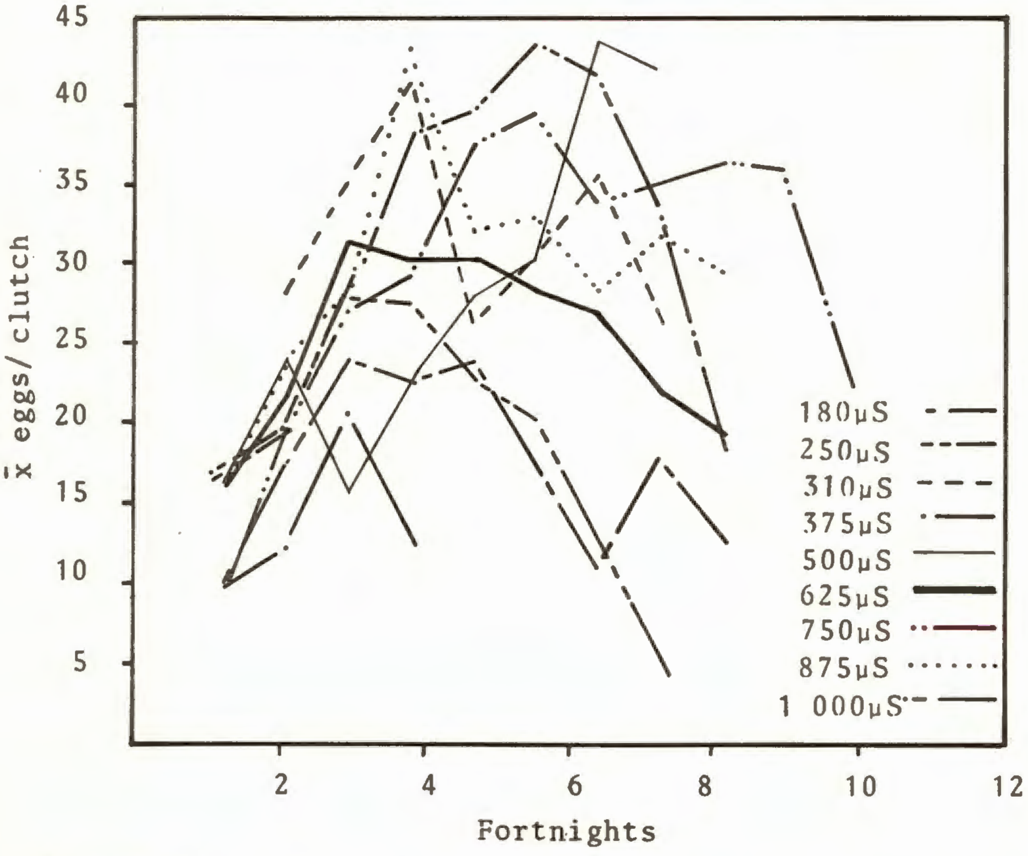


Figure 56. The mean fortnightly number of eggs per egg clutch of *B.(B.) tropicus* at the various constant conductivities based on the data contained in Appendix table 23

54 and 55 also indicates that salinity affected the number of egg clutches produced per snail more than it affected the number of eggs per egg clutch produced per fortnight by a snail. During an investigation of the substrate preferences of *B.(B.) tropicus* Combrinck (1968), in a similar analysis of egg production, also concluded that the number of egg clutches produced per snail in a certain period determines the shape of the m_x curve to a great extent.

The V_x sequence based on values calculated for the different cohorts was 625 µS > 1000 µS > 250 µS > 750 µS > 500 µS > 310 µS > 375 µS > 875 µS > 180 µS. A comparison of this sequence with the m_x sequence reveals that, with regard to V_x, the cohorts at 250 µS and 375 µS are both better placed in the V_x sequence at the cost of especially the cohorts at 750 µS and 875 µS. The cohort at 500 µS was also better placed in the V_x sequence. It is clear from figures 44 and 46 that these cohorts in question had reached their highest m_x values before serious mortalities had commenced, unlike the cohorts at 750 µS and 875 µS for which the highest m_x values were obtained after a large number of the snails had died. There is, consequently, also very little difference between the fecundity (m_x) and egg curves (V_x) of the cohorts at 250 µS and 375 µS whereas those of the cohorts at 750 µS and 875 µS do not resemble each other at all(figure 57).

The net reproductive rates (R_o) of the different cohorts are presented in table 34 and the cumulative increase of R_o per fortnight of the different cohorts is graphically presented in figure 58 from which the following R_o sequence is obvious: 625 µS > 750 µS > 1000 µS > 250 µS > 500 µS > 875 µS > 310 µS > 180 µS > 375 µS. The cohort at 625 µS yielded both the highest R_o value and the highest reproductive rate. The cohort at 750 µS was second in the R_o sequence, mainly because it had the longest reproductive period of all the cohorts of *B.(B.) tropicus* coupled with a high reproductive rate. The eventual value of R_o is chiefly determined by the reproductive rate and the duration of

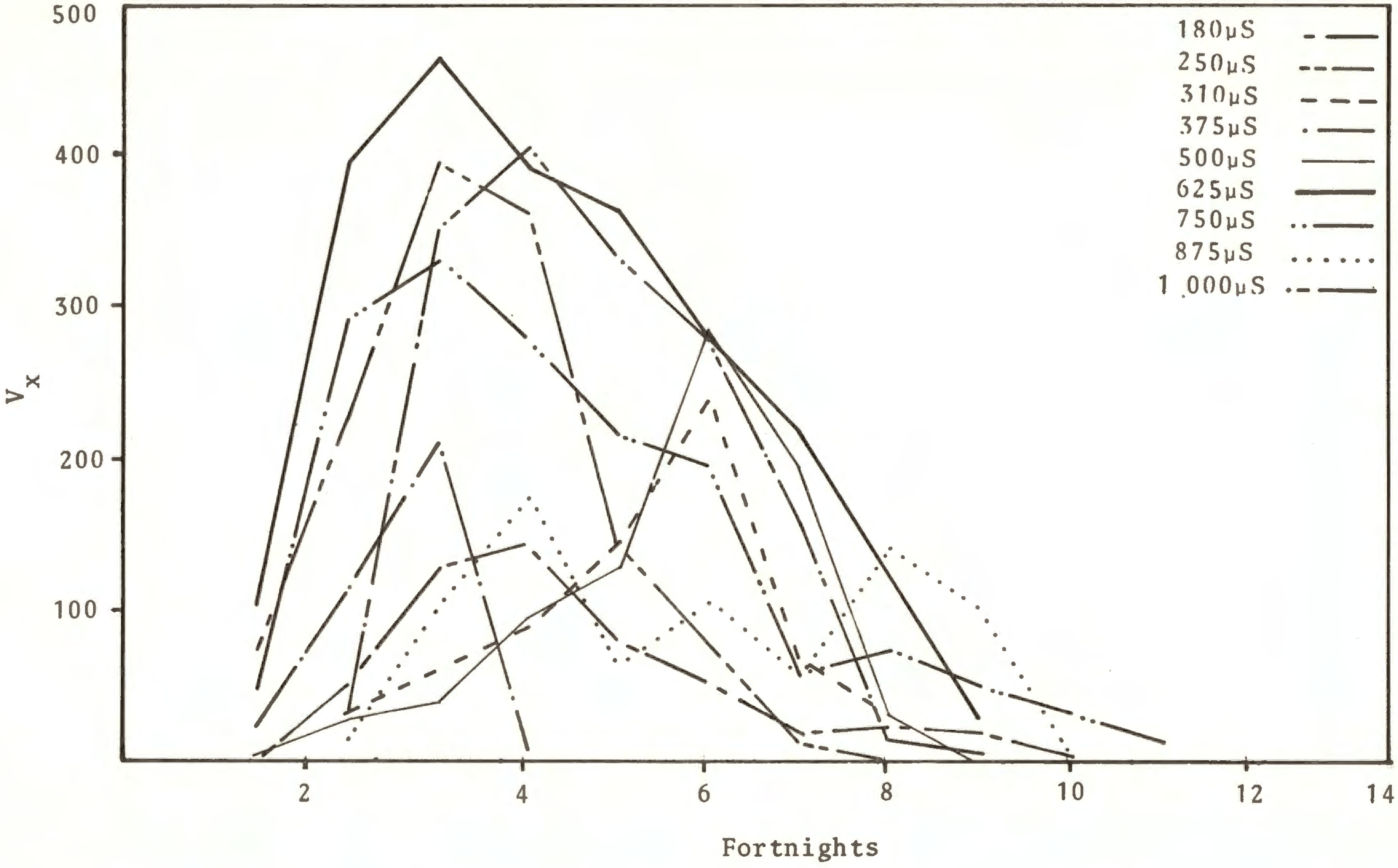


Figure 57. The V_x curves of the cohorts of *B.(B.)tropicus* at the various constant conductivities

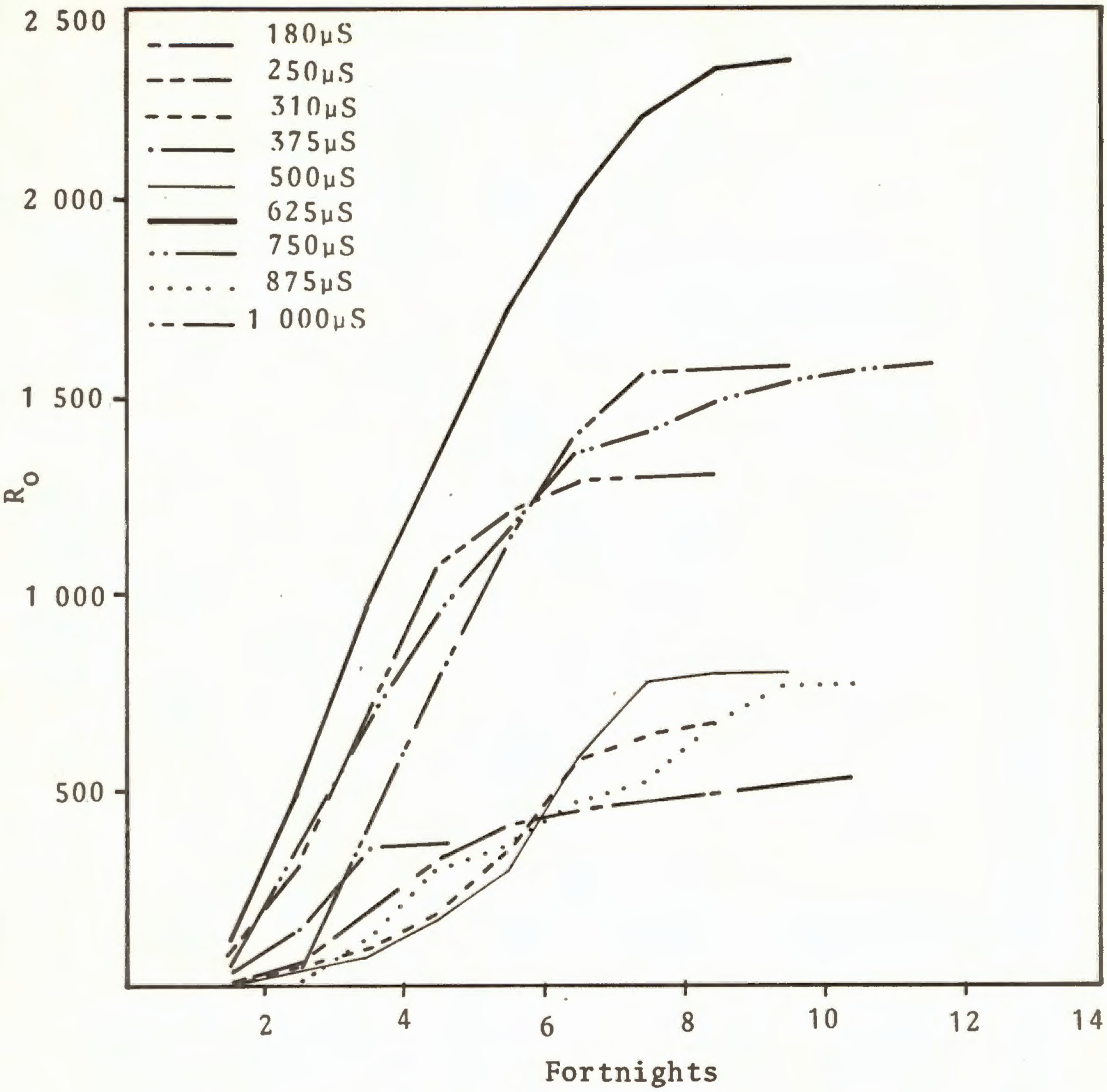


Figure 58. The increase in R_o value per fortnight of the cohorts of *B.(B.)tropicus* at the various constant conductivities

the reproductive period. A cohort with a long reproductive period can therefore achieve a higher R_o than another with a shorter reproductive period but with the same reproductive rate and vice versa. Due to its very short reproductive period the cohort at 375 µS,therefore,yielded the lowest R_o value, despite a very favourable reproductive rate. Likewise, the cohort at 180 µS, in spite of a long reproductive period, afforded a low R_o because of a very low reproductive rate.

It may, with a reasonable degree of confidence, be assumed that the T_c values calculated for the cohorts at 310 µS and 500 µS were not accurate reflections of their true T_c potentialities. These values must surely have been affected by their very low growth rates discussed elsewhere. It is, therefore, suspected that their actual T_c values would be somewhat lower than those calculated (table 34) and that they would approach those of the cohorts nearest to them in the conductivity range. With this assumption in mind it seems as if there was a tendency for the mean generation time to be shorter at the conductivities round about the middle of the range used during this experiment.

The following r_m sequence based on the data contained in table 34 can be compiled: 625 µS > 250 µS > 750 µS > 375 µS > 1000 µS > 180 µS > 500 µS > 310 µS > 875 µS. The first position occupied by the cohort at 625 µS could be attributed to the highest R_o value as well as the very high reproductive rate during the first four reproductive fortnights. These high values compensated for the not very short mean generation time (T_c) of 4,8000, which was only the third best recorded for *B.(B.) tropicus* (table 34). Although the cohort at 750 µS had a higher net reproductive rate (R_o) than the one at 250 µS the latter occupies a better position in the r_m sequence due to a better mean generation time (T_c) of 4,007. Since the cohort at 875 µS had the longest mean generation time recorded during this experiment, it afforded the lowest r_m value in spite of having a higher R_o value than the cohorts at 310 µS, 180 µS and 375 µS. It is quite clear that T_c played a decisive part in the calculation of r_m.

All r_m values calculated for this species were positive and all the λ values were higher than one. Consequently *B.(B.) tropicus* was able to survive and multiply at all those conductivities which it was subjected to during this investigation except the one at 125 µS where a very low hatching percentage was recorded and where those snails that managed to hatch failed to survive.

The results indicate that the most favourable conductivity at which to breed *B.(B.) tropicus* must be in the region of 625 µS because no other cohort yielded a λ value which could compare favourably to that of this cohort. However, the high λ values calculated at 250 µS, 375 µS and 750 µS indicate that this species should be able to maintain itself in waters with conductivities other than 625 µS. In fact it was able to survive quite comfortably and very successfully at conductivities ranging from 180 µS to 1000 µS.

3.6 Life table of *Biomphalaria salinarum* (Morelet) and *B.(P.) africanus* (Krauss)

During the final phases of the experiment specimens of *B. salinarum* and *B.(P.) africanus* were obtained from Botswana. They were collected from the Chobe River, 2 km west of the camp at Kazungula by dr. R.J. Pitchford of the Bilharzia Field Unit at Nelspruit. Initially these snails were kept in aquaria with a conductivity of ± 300 µS but it soon became clear that this conductivity was too low for them. After the conductivity was increased their performance improved and this was particularly obvious in the case of *B. salinarum.* It was consequently decided to conduct one experiment only with these two species at a conductivity of 850 µS. During this experiment they were subjected to exactly the same procedures as all other cohorts before them. It should be remembered at this point that both *B.(P.) globosus* and *B. pfeifferi* failed to survive at conducti=

Table 35 : Life table of *B. salinarum*

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	65	20	1,0000	3,2500	3,2500
2,5	1 399	20	1,0000	69,9500	69,9500
3,5	2 035	19	0,9500	107,1053	101,7500
4,5	1 181	18	0,9000	65,6111	59,0500
5,5	1 008	14	0,7000	72,0000	50,4000
6,5	886	12	0,6000	73,8333	44,3000

$R_o = \Sigma V_x = 328{,}7000$

vities higher than 750 µS. The purpose of this single experiment with *B. salinarum* and *B.(P.) africanus* was, therefore, to determine whether they were capable of tolerating higher conductivities than both *B. pfeifferi* and *B.(P.) globosus* had been able to do.

Life table of *B. salinarum*

Ninety two percent of the eggs hatched within six days and the first eggs were produced 26 days later. This hatching time was one day shorter than the shortest hatching time recorded for *B. pfeifferi*. A high survival rate was displayed as well as the characteristic *Biomphalaria* mortality pattern (figure 59 and table 35) where low initial mortalities were followed by a sharp increase in the death rate. The highest m_x and V_x values were reached during the fourth fortnight. Due to the low initial mortalities there is not a great difference between the fecundity and egg curves.

Table 36

Population statistics of *B. salinarum*

λ	6,515
r_m	1,874
r_c	1,394
R_o	328,700
T_c	4,158

A comparison of the data contained in tables 18 and 36 indicates that *B. pfeifferi* achieved a better overall performance than *B. salinarum*. Nevertheless the r_m value of 1,8741 indicates that *B. salinarum* was able to survive and multiply with a great deal of success at a conductivity of 850 µS. The λ value of 6,515 implies that each member of the cohort contributed 6,515 progeny per fortnight. It obviously grew much slower than *B. pfeifferi* for its mean individual mass (appendix table 24)

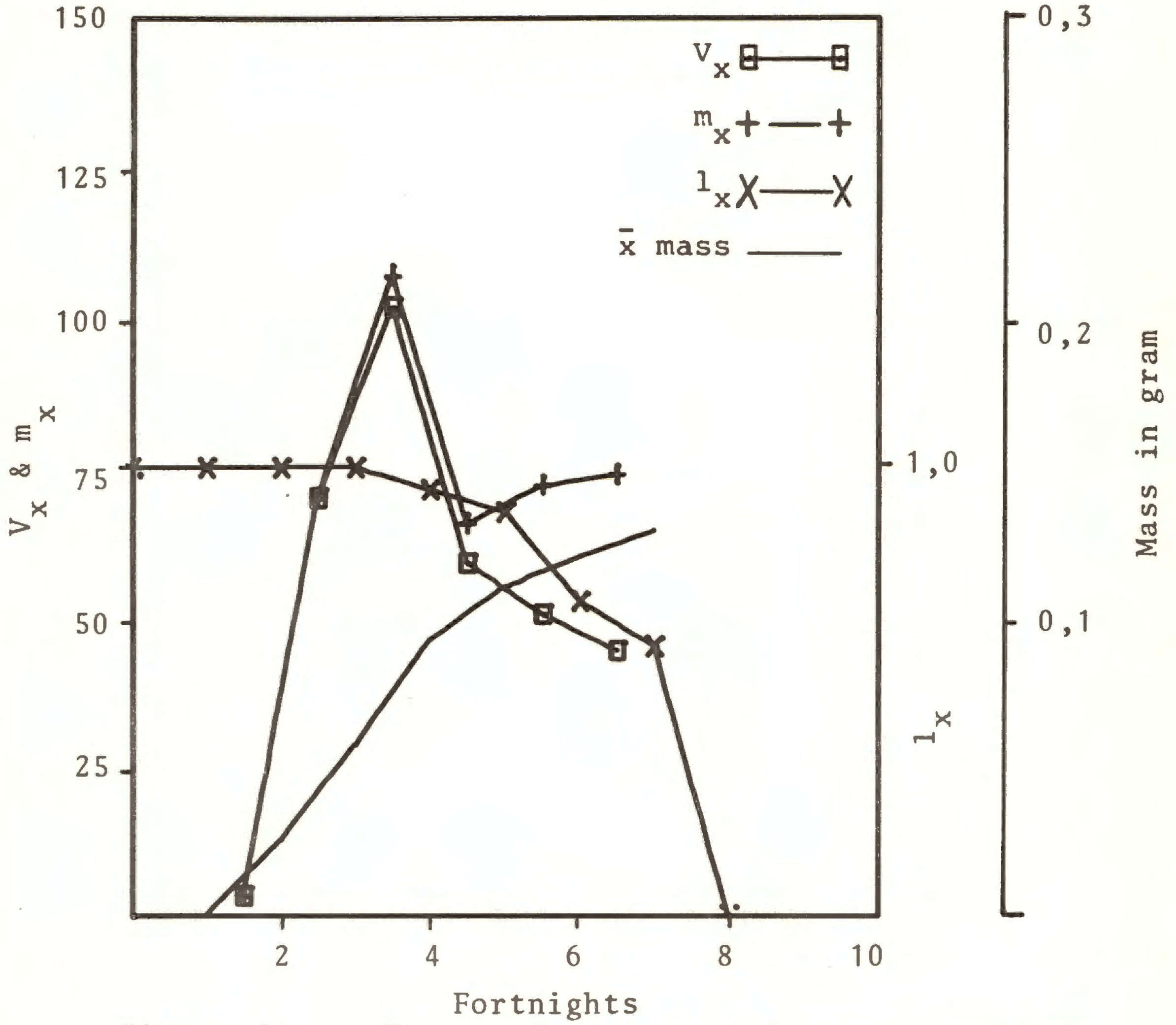


Figure 59. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.salinarum*.

Table 37 : Life table of *B.(P.) africanus*

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 315	20	1,0000	65,7500	67,7500
3,5	3 404	20	1,0000	170,2000	170,2000
4,5	4 760	19	0,9500	250,5263	238,0000
5,5	5 350	19	0,9500	281,5789	267,5000
6,5	2 970	19	0,9500	156,3158	148,5000

$R_o = \Sigma V_x = 889{,}9500$

is approximately half that attained by *B. pfeifferi* at corresponding ages (appendix table 15).

Life table of *B.(P.) africanus*

The eggs of this species took ten days to hatch, which was one day more than the longest hatching time recorded for *B.(P.) globosus* (table 10). The hatching percentage of 90% was, however, higher than that of many of the eggs of the cohorts *B.(P.) globosus*. The pre-oviposition period was a lengthy 43 days which was exceeded only by *B. pfeifferi* at 180 μS and equalled by the same species at 250 μS. Both the m_x and V_x values reached their peaks during the sixth fortnight and as a result of the very low mortality rate there was very little difference between the V_x and m_x curves (figure 60 and table 37).

Table 38

Population statistics of *B.(P.) africanus*

λ	6,307
r_m	1,842
r_c	1,416
R_o	889,950
T_c	4,795

There was very little difference between the performance of *B.(P.) africanus* at 850 μS and the best performances of *B.(P.) globosus* at any of the conductivities tested (tables 10 and 38). The r_m of 1,842 almost matched the highest equivalent r_m values attained by *B.(P.) globosus*. The high r_m achieved by *B.(P.) africanus* was the result of substantial egg production throughout coupled with a low T_c value and mortality rate. On the whole the mean individual fortnightly masses were better than those of *B.(P.) globosus* which surpassed it only at 310 μS.

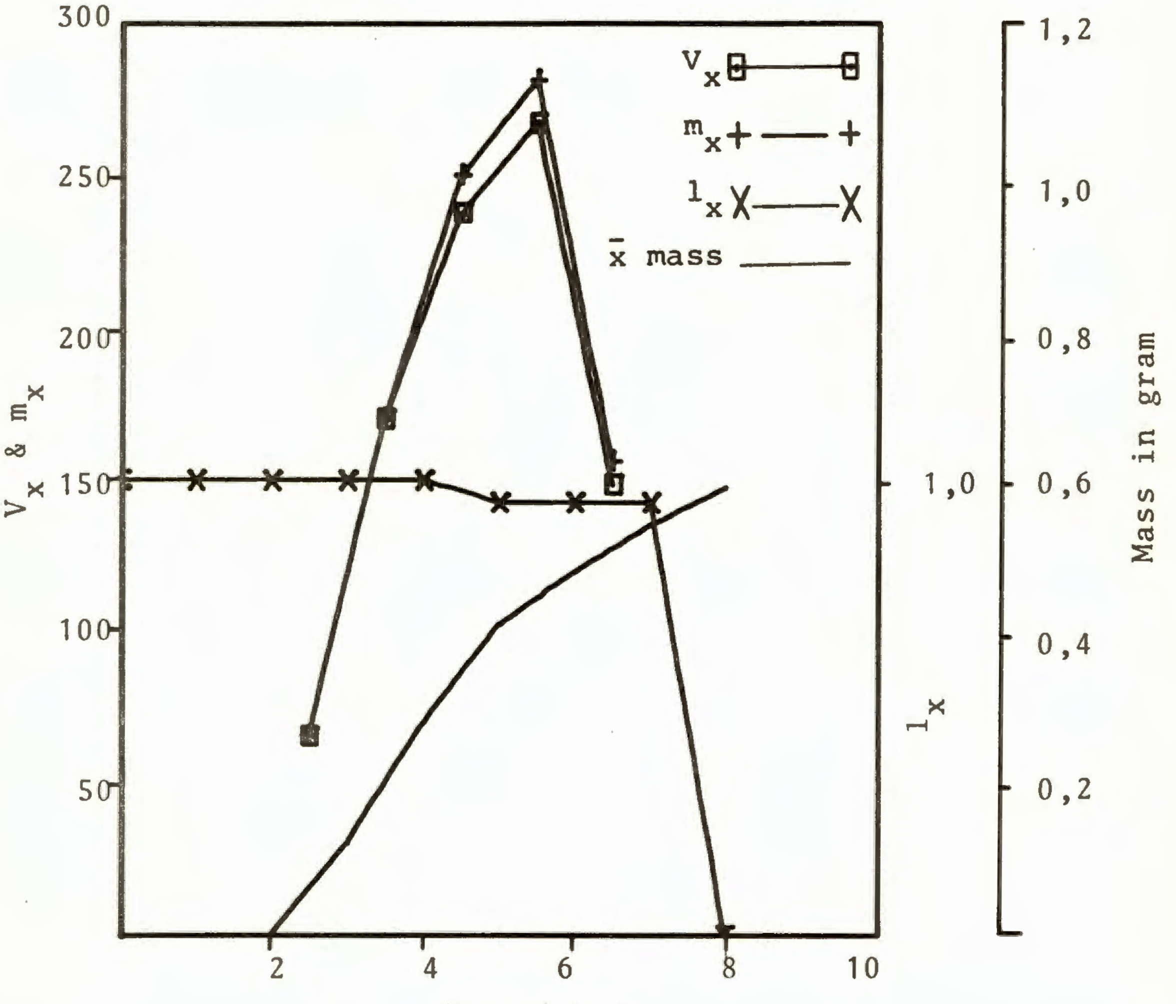


Figure 60. V_x, m_x, 1_x values and mean fortnightly mass per snail of *B.(P.)africanus*.

(appendix tables 12 and 24).

As *B. salinarum* and *B.(P.) africanus* were only subjected to one conductivity no conclusions can be reached about their optimum conductivities. As such these results should only be regarded as a reflection of their performance at a high salinity. The good performances of these two species at a conductivity where their closest relatives were unable to breed, distinguish them from *B. pfeifferi* and *B.(P.) globosus* and it may not be unreasonable to expect their optimum conductivities to be higher than those of the other two species. Furthermore, the high r_m values recorded for them at 850 μS might indicate that their upper limits of tolerance to salinity might be considerably higher than 850 μS. This would enable them to exploit waters such as small ponds which are subject to very high seasonal evaporation whereby sharp increases in the conductivity may be induced. A closer study of their distribution and habitats should confirm whether this is indeed so.

3.7 The effect of decreasing salinities in one generation

Snails are quite often recovered from natural waters with either higher or lower conductivities than those at which it had been possible to breed them in the laboratory during the present investigation. It may, furthermore, be accepted as a fact that, in many natural habitats, the conductivity does not remain constant throughout the lifespan of one generation. Thus, a decrease in the conductivity of natural waters results from dilution by rainwater while evaporation induces an increase in conductivity in many habitats. Seventy five percent of the waters sampled by Schutte & Frank (1964) in the South Eastern Transvaal and Swaziland, for instance, fall into a category with a mean conductivity of 54 μS. According to observations made during the foregoing experiments this seems to be definitely unfavourable for most species. In spite of these low conductivities these waters frequently support large and thriving snail colonies and Alves (1956) finds it remarkable that snails can continue to exist, to grow and bear shells in waters which should theoretically be grossly unfavourable to them.

The ability of *B.(P.) africanus* to survive changes in the concentration of dissolved solids in the water in which they are living, has also been studied by Heeg (1975). He observed that the transfer of a sample of these snails from water in their natural habitat containing 490 ppm total dissolved solids to a laboratory culture medium of 126 ppm total dissolved solids was accompanied by a marked increase in the variability of the rate of oxygen consumption among individuals and a 46% mortality. Transfer through the same gradient, but through two acclimatory stages of intermediate dissolved solid content, eliminated both these effects, suggesting an ability to acclimate and therefore to cope with the more gradual changes which may be expected to occur under field conditions where drastic changes must be rare. The results presented by Heeg (1975) indicate that *B.(P.) africanus* is adapted to withstand gradual changes, at least such as those caused by dilution of the medium by rain.

Heeg concludes that the observations of Schutte & Frank (1964) who could find no relation between the distribution of freshwater snails and the composition of the dissolved solid content of natural waters, can be explained by this capacity to acclimate to different conditions.

Similarly, flourishing snail populations sometimes occur in waters with very high conductivities. Harry & Aldrich (1958) collected *B. glabrata* from waters with dissolved solid concentrations of up to 3 000 ppm and Watson (1958) reports the survival of *B. truncatus* in water containing 1 500 ppm dissolved chlorides and, subject to acclimation, the tolerance of even higher salinities. Brumpt (1941) maintains that *B. glabrata* could be transferred from a habitat with a low concentration of solids to one containing a high concentration by progressively acclimating the snails to the new habitat. Pimentel & White (1959) is of opinion that the osmoregulatory system of *B. glabrata* is not well adapted to rapid changes in the electrolyte content of the water, even when the tolerance of the species is not exceeded.

During the present experiments the only species that could be bred below a conductivity of 180 µS was *L. natalensis* and only *B.(B.) tropicus* could be bred above 750 µS. Judging from previous results (Jennings et al., 1973) obtained with *B. pfeifferi* there appears to be a minimum and maximum threshold value for dissolved salts above and below which eggs either do not hatch or at which the juveniles are unable to survive. Similar observations were made for *B. glabrata* by Harry et al. (1957) and by Watson (1958) for *B.(B.) truncatus*. The conditions in question are usually more lethal to the eggs and young snails than to the adults and may consequently limit the occurrence and therefore distribution of the species by their effect on breeding. As long as the duration of these adverse conditions do not exceed the reproductive life of the adult population, the continued existence of the species is, however, not endangered.

On account of the foregoing observations an attempt was made to determine the effects of stepwise increasing and stepwise decreasing conductivities on the species experimented with. Two recirculating systems containing water with a conductivity of 250 µS were stocked with the eggs of *L. natalensis, B.(P.) globosus, B.(B.) tropicus* and *B. pfeifferi*. During the preceding experiments it was ascertained that water with this conductivity was favourable to all four species. After all the cohorts in each aquarium had completed at least one fortnight of egg production the conductivities of the two systems were respectively increased and decreased. The decrease was accomplished by the addition of distilled water to the recirculating system and an increase was managed by the addition of quantities of water with a high conductivity. In this way the conductivity of one aquarium was stepwise lowered to 50 µS and maintained at this level for the duration of the snails' lives while the conductivity in the other aquarium was increased stepwise over a period of six weeks and maintained at 980 µS. The extent of the stepwise changes as well as the period over which they were created is graphically expounded in figures 61 to 68. Egg production and growth rates were determined for all cohorts in this experiment.

If decreasing conductivities affect the snails in any way this should be revealed by comparing their performance under these experimentally changing conductivities with that of the same species kept at its optimum constant conductivity. This had to be done because the conductivity was regularly being decreased so that no specific conductivity could be singled out as the one which actually affected the snails. Consequently this overall performance can, at best, only be compared with that of the same species at it's optimum constant conductivity. Furthermore, no or very slight differences in the performance might obviously reflect only the ability of these snails to tolerate changing conductivities while any statistically significant divergence from the performance recorded at the optimum constant conductivity should indicate the opposite. Since all the snails being subjected to decreasing and increasing conductivities had already reached reproductive age the results only apply to adult snails. The adverse effects of certain low and high conductivities on eggs and juveniles reported on elsewhere, can therefore be ruled out.

Lymnaea natalensis

The cohort of this species at its optimum constant conductivity of 250 µS yielded a r_m value of 2,1358 (table 24) and it is clear that the r_m value of 2,0008 calculated for the cohort at 250 –> 50 µS compares quite favourably to this (table 47). Despite this agreement there are certain aspects which should be remarked on.
The egg production of the cohort at 250 µS was much higher than that of the one at 250 µS –> 50 µS and a comparison of the data in tables 21 and 39 reveals that although both cohorts did practically equally well during the fourth fortnight the one at 250 –> 50 µS lagged behind after this. At this stage of the

Table 39 : Life table of *L. natalensis* at stepwise decreasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 720	20	1,0000	86,0000	86,0000
3,5	8 400	20	1,0000	420,0000	420,0000
4,5	6 159	20	1,0000	307,9500	307,9500
5,5	2 372	18	0,9000	131,7778	118,6000
6,5	1 075	13	0,6500	82,6923	53,7500
7,5	725	5	0,2500	145,0000	36,2500
8,5	671	4	0,2000	167,7500	33,5500
9,5	172	3	0,1500	57,3333	8,5999
10,5	0	1	0,0500	0	0

$R_o = \Sigma V_x = 1\ 081{,}6990$

experiment the conductivity was approaching 100 µS, and thereby entered a range (figure 61) decidedly unfavourable for *L. natalensis*. Although egg production dropped rapidly after the fifth fortnight members of this cohort survived for six fortnights at

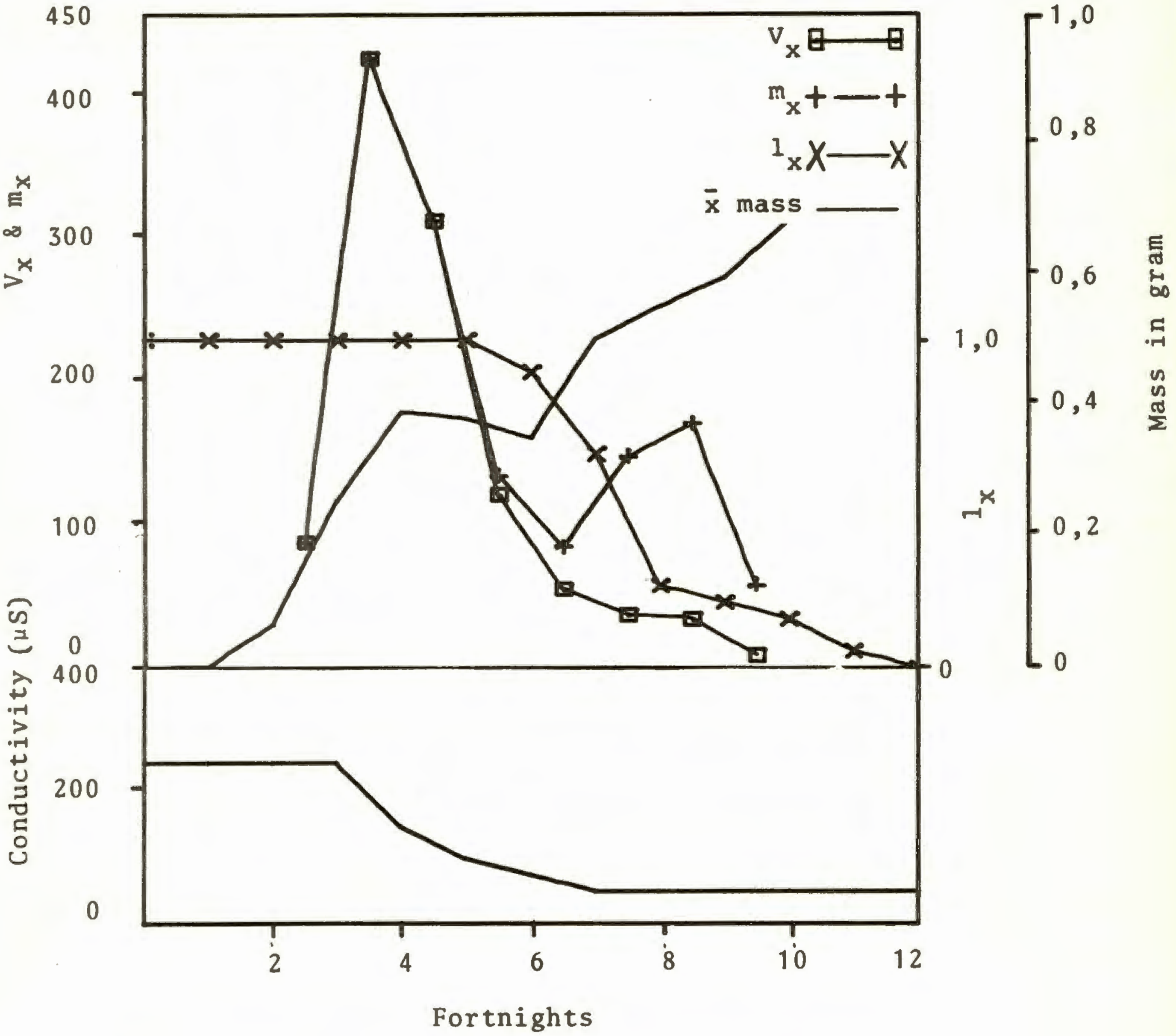


Figure 61. V_x, m_x, l_x values and mean fortnightly mass per snail of *L. natalensis* being subjected to a stepwise decrease in conductivity

conductivities considerably below 100 μS (figure 61). They, therefore, survived longer than the cohort at 250 μS which survived for eight fortnights. Despite its poor survival, however, the cohort at 250 μS showed a higher net reproductive rate (R_0) (tables 24 and 47) which was mainly the result of sustained high reproduction during the phase in which reproduction by the cohort at 250 –> 50 μS dwindled. The drop in egg production of the latter cohort and possibly also the increase in mortalities after the seventh fortnight might possibly have been caused by the conductivity dropping to too low a level. At the lower conductivities therefore only egg production seemed to be affected.

Biomphalaria pfeifferi

It has been concluded earlier on that the optimum conductivity for *B. pfeifferi* lies somewhere between 375 μS and 500 μS but it was also concluded that this species was not very sensitive to reasonable conductivity changes within the range of 180 μS and 750 μS (table 18). Attempts to breed *B. pfeifferi* at 100 μS during the present experiments met with no success but during previous experiments (Jennings et al., 1973) breeding at this conductivity was more successful yielding a r_m value of 0,4982. Compared to the r_m values contained in tables 18 and 47 this was very low and could, therefore, indicate that a conductivity of 100 μS was very close to the lower limit of the salinity tolerance of *B. pfeifferi*.

In the present experiment, the conductivity was kept at 250 μS for three fortnights (figure 62) after which it was stepwise decreased over a period of four fortnights to 50 μS. During the firtst seven fortnights the mortality rate was very low but as the conductivity approached 50 μS this increased to some extent (figure 62) and table 40). This mortality pattern, however, cannot be regarded as being significantly different from that of the cohort at 500 μS (figure 21). What might be noteworthy is the fact that the lowering of the conductivity from 150 μS to 50 μS resulted in a burst of egg production un=

Table 40 : Life table of *B. pfeifferi* at stepwise decreasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	1 786	20	1,0000	89,3000	89,3000
2,5	7 061	20	1,0000	353,0500	353,0500
3,5	8 261	20	1,0000	413,0500	413,0500
4,5	9 645	19	0,9500	507,6315	482,2499
5,5	10 004	19	0,9500	526,5300	500,2035
6,5	5 617	16	0,8000	351,0625	280,8500
7,5	4 466	14	0,7000	319,0000	223,3000
8,5	5 061	12	0,6000	421,7500	253,0500
9,5	6 795	11	0,5500	566,2500	311,4375
10,5	4 746	11	0,5500	431,4545	237,3000
11,5	0	5	0,2500	0	0

$R_o = \Sigma V_x = 3\ 162{,}7909$

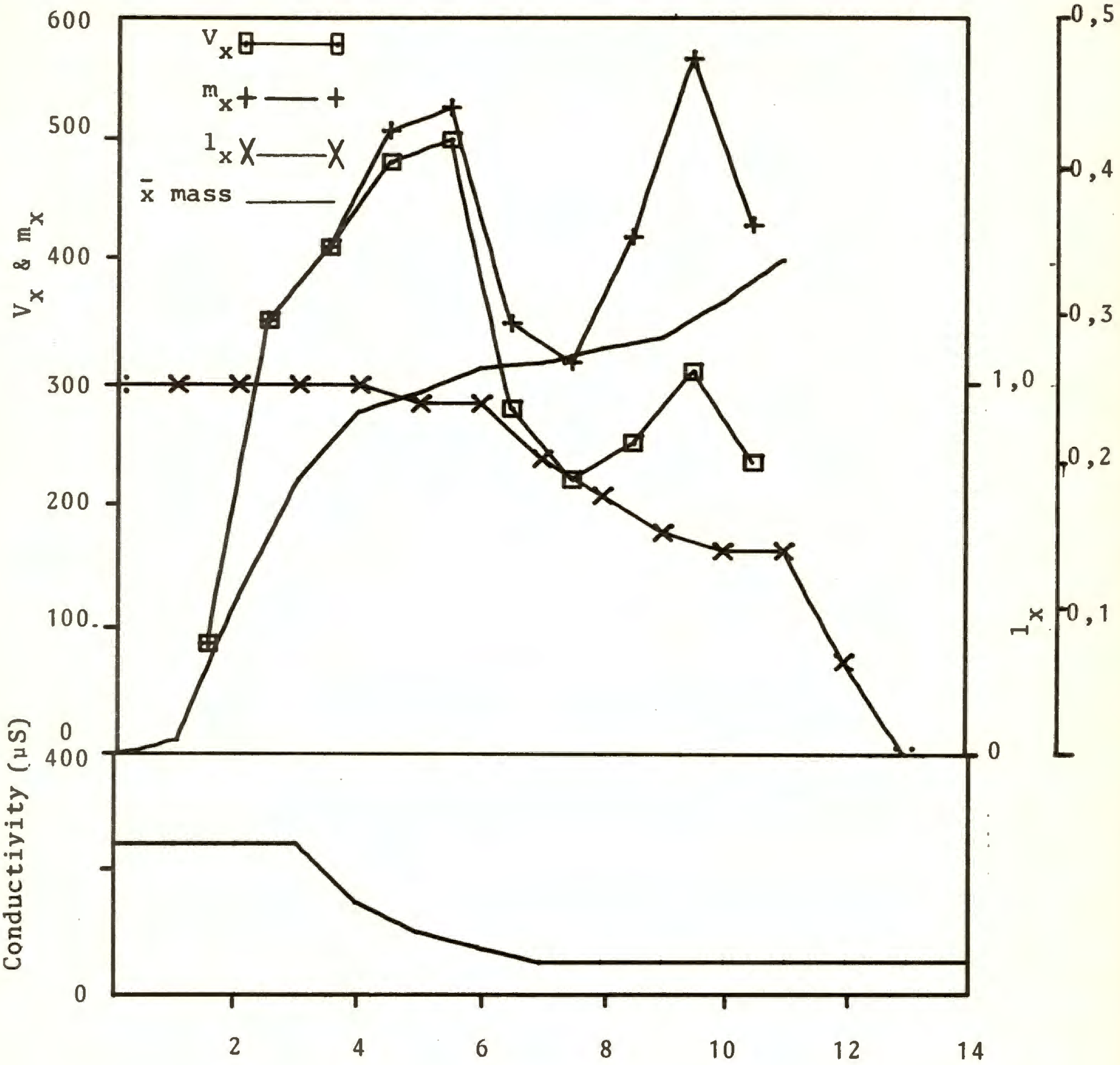


Figure 62. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.pfeifferi* being subjected to a stepwise decrease in conductivity

equalled by any other cohort of *B. pfeifferi* during these experiments (table 40 and figure 62). This observation supports that of Combrinck (1968) who observed similar reactions to reduced conductivity by *B.(B.) tropicus* and *L. natalensis*. As a result of its very high reproductive rate this cohort achieved the highest net reproductive rate (R_0) of all the cohorts of *B. pfeifferi* studied during this investigation.

A comparison of the growth rates of all the investigated cohorts of *B. pfeifferi* indicates (appendix tables 15 and 26) that the cohort at 250 –> 50 µS reached the highest mean mass per snail. The snails at 180 µS nearly equalled this growth rate and the very high growth rates recorded for the snails at these lower conductivity ranges suggest that these conditions promote rapid growth subject, however, to the condition that the snails had first reached a certain minimum size before being exposed to the low conductivities. It would, therefore, seem as if lowering of conductivity such as might in nature be caused by flooding of the habitat, has a definite beneficial effect on the growth and egg production of *B. pfeifferi*. This benefit would, however, be of no avail if the conditions of low salinity persisted for very long periods because of the detrimental effect low salinities have on the hatching of eggs and also on the hatchlings themselves.

Bulinus (P.) globosus

According to Schutte & Frank, (1964) just over 75% of the waters in the South Eastern Transvaal and Northern Swaziland fall into the soft or very soft category with mean conductivities of 54 µS and 103 µS respectively. The highest mean conductivity encountered by them in these areas was 696 µS. Brown (1966) considers these areas and the north eastern part of Natal to be the main distributional area of *B.(P.) globosus*. Conductivities in the latter area were found to vary between 85 µS and 600 µS (personal observation). As a result of the predominance in these areas of waters with low salinities it may be assumed that *B.(P.) globosus*

Table 41 : Life table of *B. (P.) globosus* at stepwise decreasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	860	20	1,0000	43,0000	43,0000
3,5	3 494	20	1,0000	174,7000	174,7000
4,5	5 312	20	1,0000	265,6000	265,6000
5,5	5 694	19	0,9500	299,6842	284,7000
6,5	4 704	18	0,9000	261,3333	235,1999
7,5	2 923	16	0,8000	182,6875	146,1500
8,5	2 261	15	0,7500	150,7333	113,0499
9,5	1 003	12	0,6000	83,5833	37,7333
10,5	566	9	0,4500	62,8889	28,3000
11,5	418	7	0,3500	59,7143	20,9000
12,5	52	3	0,1500	17,3333	2,5999

$R_o = \Sigma V_x = 1\ 371{,}9330$

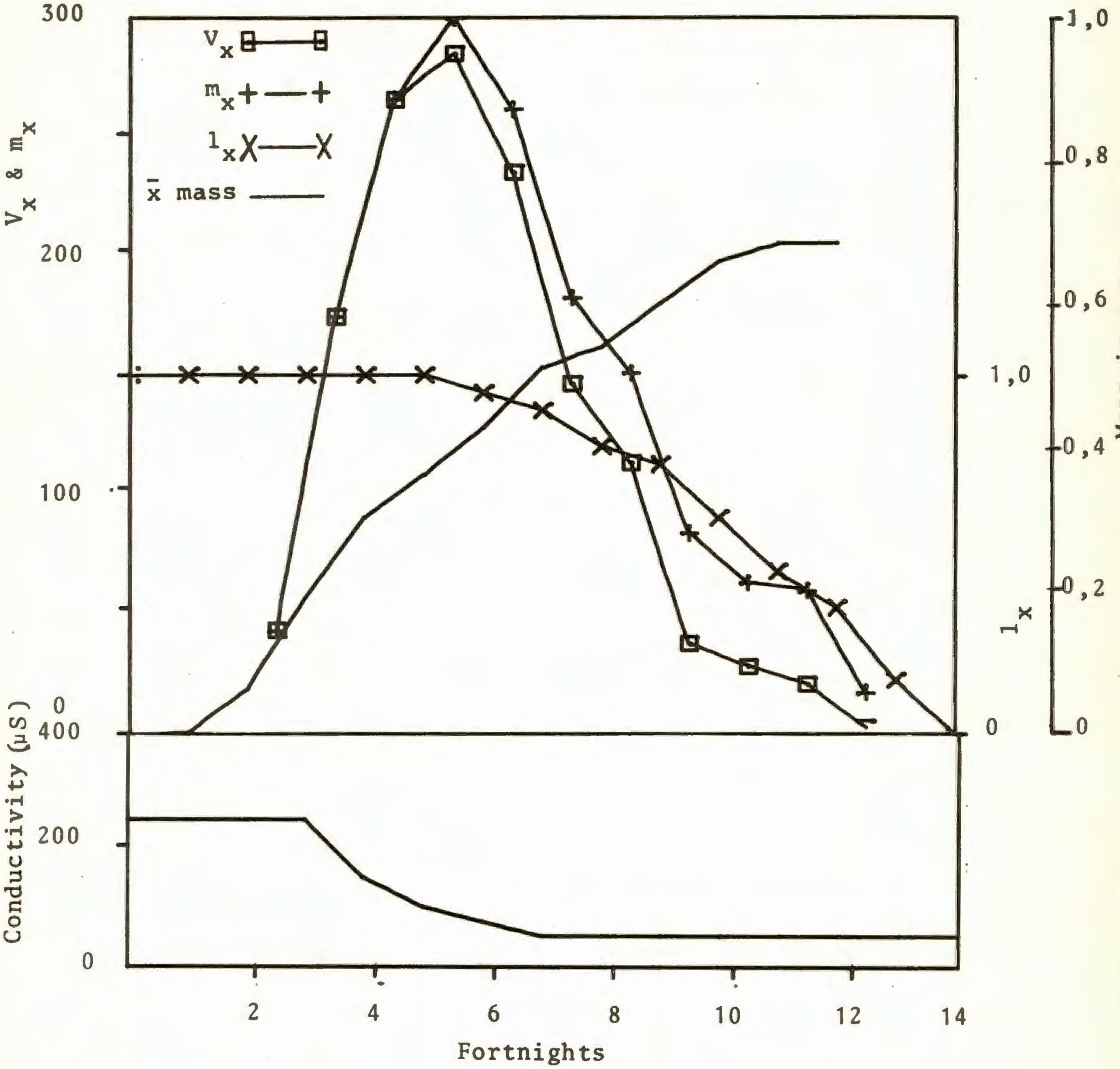


Figure 63. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.(P.)globosus* being subjected to a stepwise decrease in conductivity

must be adapted to these conditions.

Although laboratory attempts to breed this species at conductivities lower than 180 µS failed, the assumption made above proved to be true for the adult specimens which were subjected to decreasing conductivities. The high initial egg production at 250 µS was maintained (table 41) and the mortality pattern did not differ very much from that of the cohort at the optimum constant conductivity of 310 µS (figure 5 and 63). There was practically no difference in the R_0 values of the two cohorts (250 —> 50 µS and 310 µS) (tables 10 and 47) and in respect of their growth rates the cohort at 310 µS enjoyed only a slight advantage (appendix tables 12 and 26).

Judging from these results it is clear that, as in the case of *B. pfeifferi*, decreasing salinities seem to have no ill effect on *B.(P.) globosus* once the snails had reached a certain age.

Bulinus (B.) tropicus

During the first part of this project the optimum conductivity at which to breed *B.(B.) tropicus* was found to be in the region of 625 µS. This was the highest optimum conductivity determined for any of the four species experimented with. It was, however, not altogether unexpected in view of the nature of many of the habitats frequently occupied by this species which include temporary waters with very high salinities. Lowering of the conductivity could therefore be expected to be detrimental to the snails especially below a certain level.

In the present experiment a low hatching percentage of 45,87% was recorded and egg production started 26 days after hatching (table 47) both these values were not as good as those of the cohort at 250 µS (table 34) and, therefore, seem to confirm the conclusion that 250 µS, although not deleterious for *B.(B.) tropicus*, was definitely sub-optimal. Down to a conductivity of 150 µS (figure 64 and table 42) no drastic changes in perfor=

Table 42 : Life table of *B. (B.) tropicus* at stepwise decreasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	54	20	1,0000	2,7000	2,7000
2,5	4 636	20	1,0000	231,8000	231,8000
3,5	7 787	17	0,8500	458,0588	389,3499
4,5	4 425	17	0,8500	260,2941	221,2499
5,5	2 414	12	0,6000	201,1667	120,7000
6,5	170	11	0,5500	15,4545	8,4999
7,5	0	10	0,5000	0	0
8,5	0	7	0,3500	0	0

$R_o = \Sigma V_x = 989{,}2997$

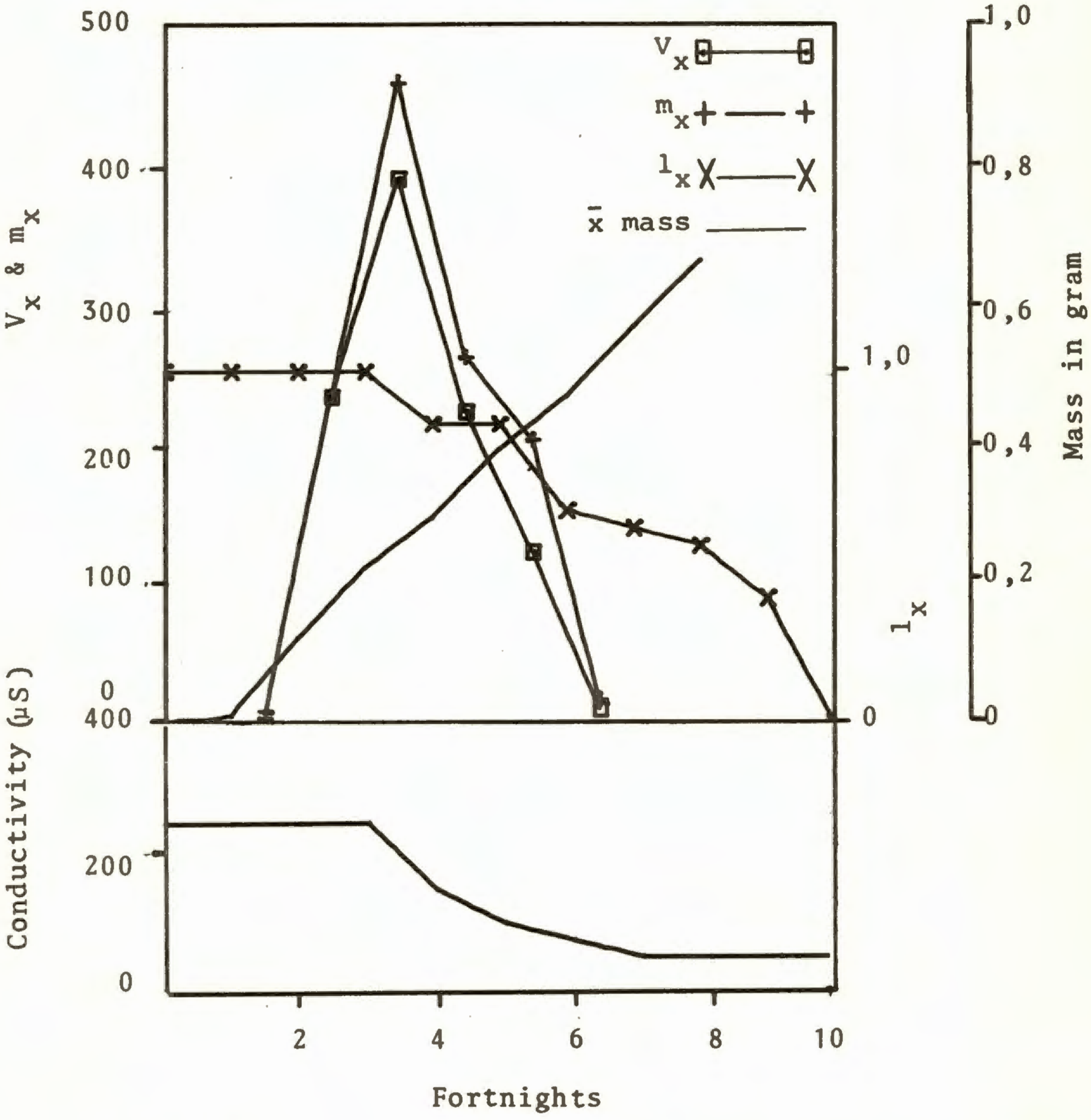


Figure 64. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.(B.)tropicus* being subjected to a stepwise decrease in conductivity

mance of the snails occurred, but once it started dropping below 100 µS egg production fell sharply and after one week at 50 µS ceased completely. Consequently no eggs were produced during the last two fortnights (figure 64 and table 42). The mortality pattern remained practically unchanged and there was also no harmful effect on the growth rate which was actually better than that of the cohort at 625 µS (appendix tables 21 and 26). The only negative effect, therefore, which could be attributed to the low conductivity was that on egg production.

The results obtained from this experiment indicate that survival was practically unaffected in all four species until the conductivity approached the region of 50 µS. In the cases of *L. natalensis* and *B.(B.) tropicus* egg production was detrimentally affected after the conductivity had decreased below 100 µS but in the cases of *B. pfeifferi* and *B.(P.) globosus* this was not the case. On the contrary, the lowering of the conductivity had a benificial effect on the oviposition of *B. pfeifferi* in that it resulted in an upsurge of egg production.

3.8 The effect of stepwise increasing in one generation

Lymnaea natalensis

A conductivity of 150 µS was previously found to be very close to the optimum conductivity required by this species. Both the hatching percentage of 96% and the hatching time of 10 days recorded for the cohort subjected to increasing salinities were practically the same as those of the cohort at 250 µS (tables 24 and 48). Egg production of the former, however, started five days later than that of the latter. Mortalities set in during the fortnight chosen for the first salinity increase (figure 65 and table 43) and eight fortnights later all the snails had died. At this stage the conductivity had reached 750 µS. The cohort at 250 µS also survived for eight fortnights which was more or less the survival period of all the cohorts of *L.natalensis*. On the basis of

Table 43 : Life table of *L. natalensis* at stepwise increasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	831	20	1,0000	41,5500	41,5500
3,5	1 758	17	0,8500	103,4118	87,9000
4,5	1 116	15	0,7500	74,4000	55,8000
5,5	451	13	0,6500	34,6923	22,5499
6,5	62	11	0,5500	5,6364	3,1000
7,5	0	6	0,3000	0	0

$R_o = \Sigma V_x = 224{,}8999$

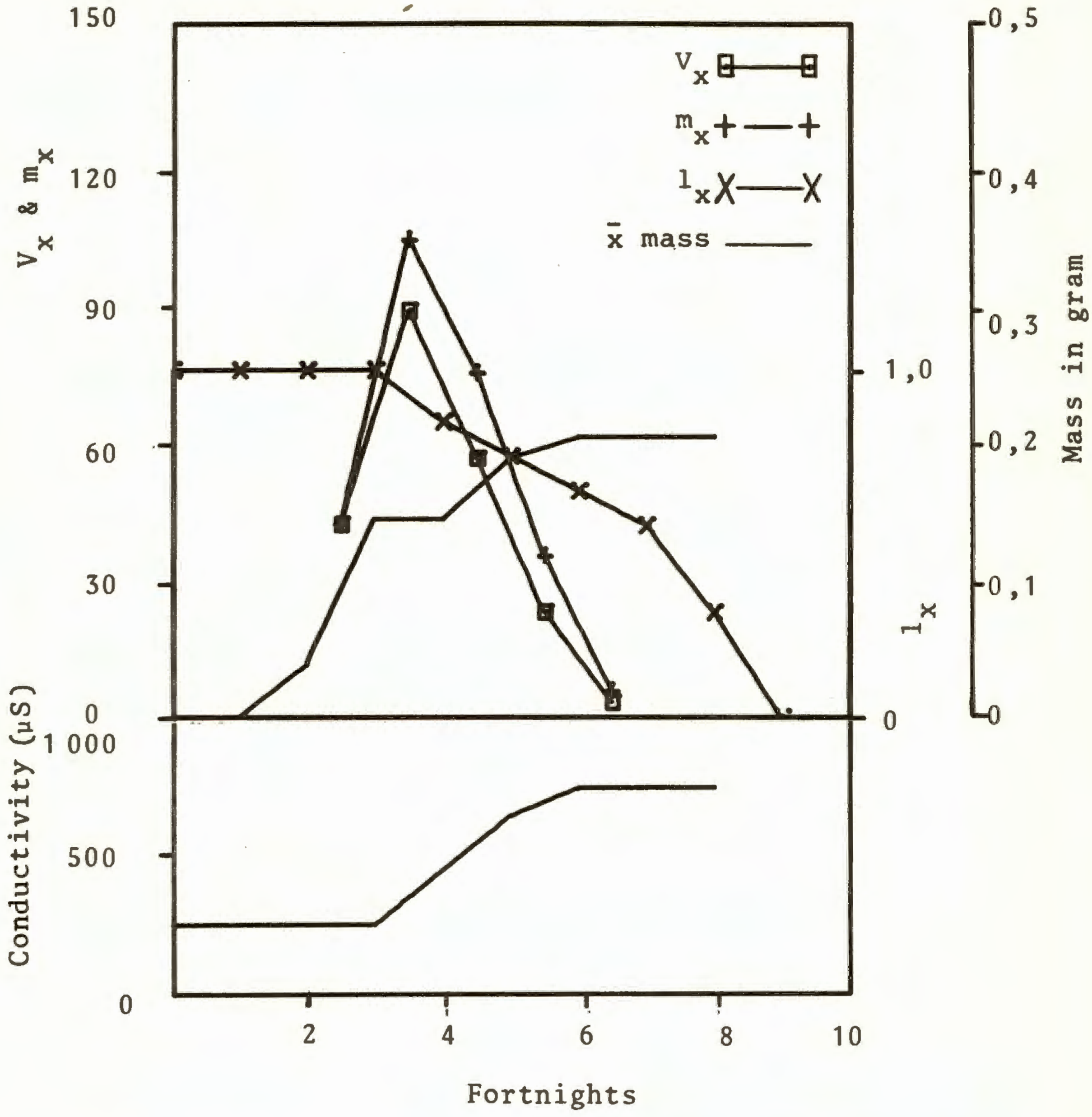


Figure 65. V_x, m_x, l_x values and mean fortnightly mass per snail of *L.natalensis* being subjected to a stepwise increase in con= ductivity

the data in tables 43 and 21 the main difference between these two cohorts lay in the egg production which was much lower in the cohort at 250 –> 1 000 µS. This becomes very obvious when the net reproductive rates are compared (tables 24 and 48). The growth rates also differed considerably and seem to have been suppressed by the increasing salinities. In the case of adult *L. natalensis* it therefore appears that as in the case of the eggs and hatchlings of this species, salinity above a certain critical level has a detrimental effect. This effect is manifested mainly by a drop in egg production and growth rate. The mortality pattern does not show any of the conductivities used as having been lethal to this species.

Biomphalaria pfeifferi

Although the hatching time was longer than in any other cohort of *B. pfeifferi* this one had the shortest pre-oviposition period of all (tables 18 and 48). A hatching percentage of 90,86% which was slightly higher than that of the cohort at 250 µS was recorded. The very high r_m value of 3,6786, which was the highest recorded for any cohort of *B. pfeifferi*, could be attributed to the high egg production during the first two reproductive fortnights but mainly to that of the first reproductive fortnight. The egg production, however, did not change notably with increasing conductivity (table 44). The mortality pattern differed from that which characterized the other cohorts of this species, for a steady mortality occurred throughout the experiment (table 44 and figure 66). Nevertheless, when all factors selected for observation are considered it seems as if increasing salinity up to the level reached in this experiment did not affect *B. pfeifferi* in any significant manner.

Bulinus (P.) globosus

These eggs took three days longer to hatch than the ones at 250 µS but the hatching percentage was higher and the pre-ovipo=

Table 44 : Life table of *B. pfeifferi* at stepwise increasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	4 752	20	1,0000	237,6000	237,6000
2,5	8 991	20	1,0000	449,5500	449,5500
3,5	4 463	20	1,0000	223,1500	223,1500
4,5	3 257	17	0,8500	191,5882	162,8499
5,5	3 352	12	0,6000	279,3333	167,6000
6,5	2 912	12	0,6000	242,6667	145,6000
7,5	2 466	8	0,4000	308,2500	123,3000
8,5	1 369	5	0,2500	273,8000	68,4500
9,5	377	2	0,1000	188,5000	18,8500
10,5	0	2	0,1000	0	0

$R_o = \Sigma V_x = 1\ 614{,}9400$

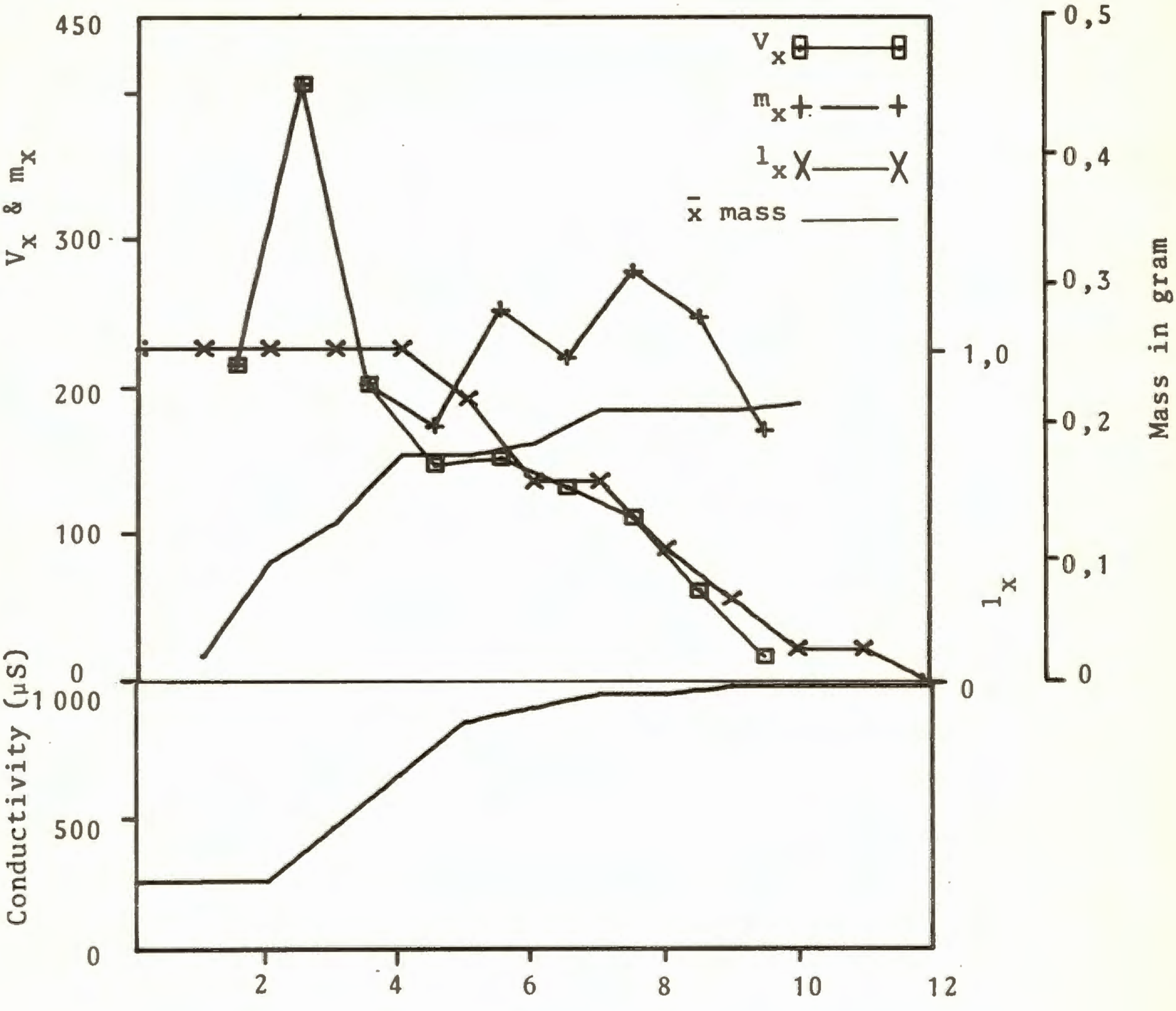


Figure 66. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.pfeifferi* being subjected to a stepwise increase in con= ductivity

sition period considerably shorter (tables 10 and 48). The conductivity was controlled at 250 µS for three fortnights after which it was raised. During the first five fortnights the mortality rate remained very low and during the first two reproductive fortnights egg production was as could be expected for *B.(P.) globosus* although that of the second reproductive fortnight was not as high as that of the cohort at 310 µS. The conductivity had, however, reached 450 µS during this period (table 45 and figure 67). Egg production dropped sharply after the conductivity had reached 450 µS and at 650 µS only 926 eggs were produced in one fortnight by 18 snails (table 45). After the conductivity had increased above 650 µS egg production ceased and a drastic rise in mortalities set in (figure 67) reducing the survivors to only four specimens at 850 µS. They all died before the conductivity had reached 900 µS. A comparison of the data in appendix tables 12 and 26 shows that although the snails grew normally for the first few fortnights, the growth rate slowed down considerably towards the fourth fortnight and was at this stage comparable with that of the cohort at 750 µS where performances were not good.

It seems reasonably clear that whereas *B.(P.) globosus* tolerated a sharp drop in salinity quite well rising salinities appeared to be detrimental to it.

Bulinus (B.) tropicus

The eggs took eight days to hatch and a hatching percentage of 69,68% was recorded. Egg production commenced 20 days after the snails had hatched (table 48). Although the optimum conductivity previously determined for *B.(B.) tropicus* was 625 µS, this species performed quite well at conductivities higher than this. It would therefore be not unreasonable to expect rising conductivities to have no ill effects on it. From the data in table 46 and figure 68 it appears that this was not the case for as the conductivity increased from 850 µS to 900 µs during the sixth fortnight the mortalities rose sharply. This agrees with the

Table 45 : Life table of *B. (P.) globosus* at stepwise increasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	1 097	20	1,0000	54,8500	54,8500
3,5	2 232	18	0,9000	124,0000	111,6000
4,5	926	18	0,9000	51,4444	46,3000
5,5	0	4	0,2000	0	0

$R_o = \Sigma V_x = 224,7500$

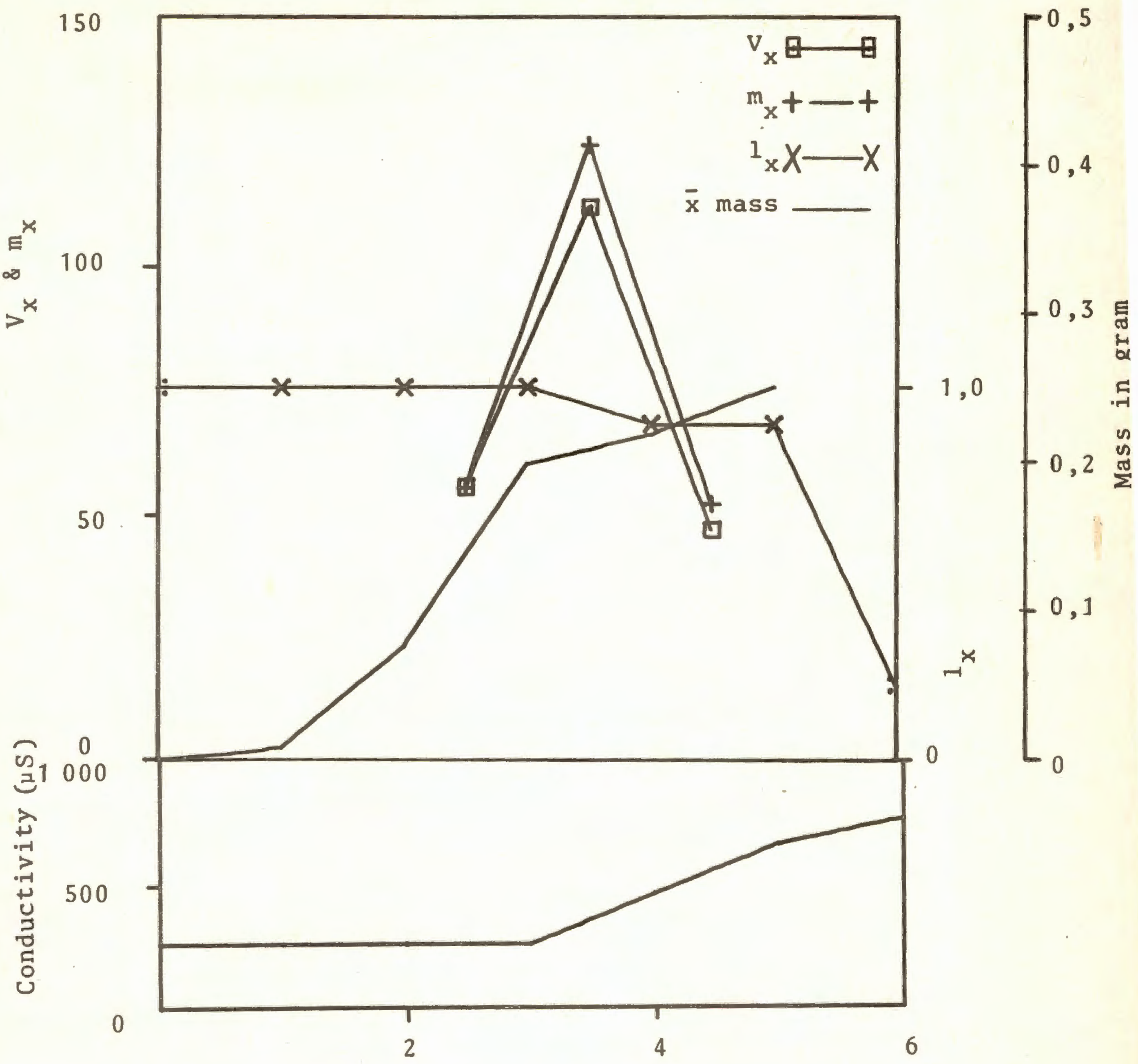


Figure 68. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.(P.)globosus* being subjected to a stepwise increase in con=ductivity

Table 46 : Life table of *B. (B.) tropicus* at stepwise increasing salinities.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	1 365	20	1,0000	68,2500	68,2500
2,5	5 826	20	1,0000	291,3000	291,3000
3,5	4 566	20	1,0000	228,3000	228,3000
4,5	2 638	17	0,8500	155,1765	131,9000
5,5	2 847	7	0,3500	406,7143	142,3500
6,5	2 505	7	0,3500	357,8571	125,2499
7,5	1 184	4	0,2500	296,0000	74,0000
8,5	800	3	0,1500	266,6667	40,0000
9,5	299	3	0,1500	99,6667	14,9500
10,5	0	1	0,0500	0	0

$R_o = \Sigma V_x = 1\ 134{,}2999$

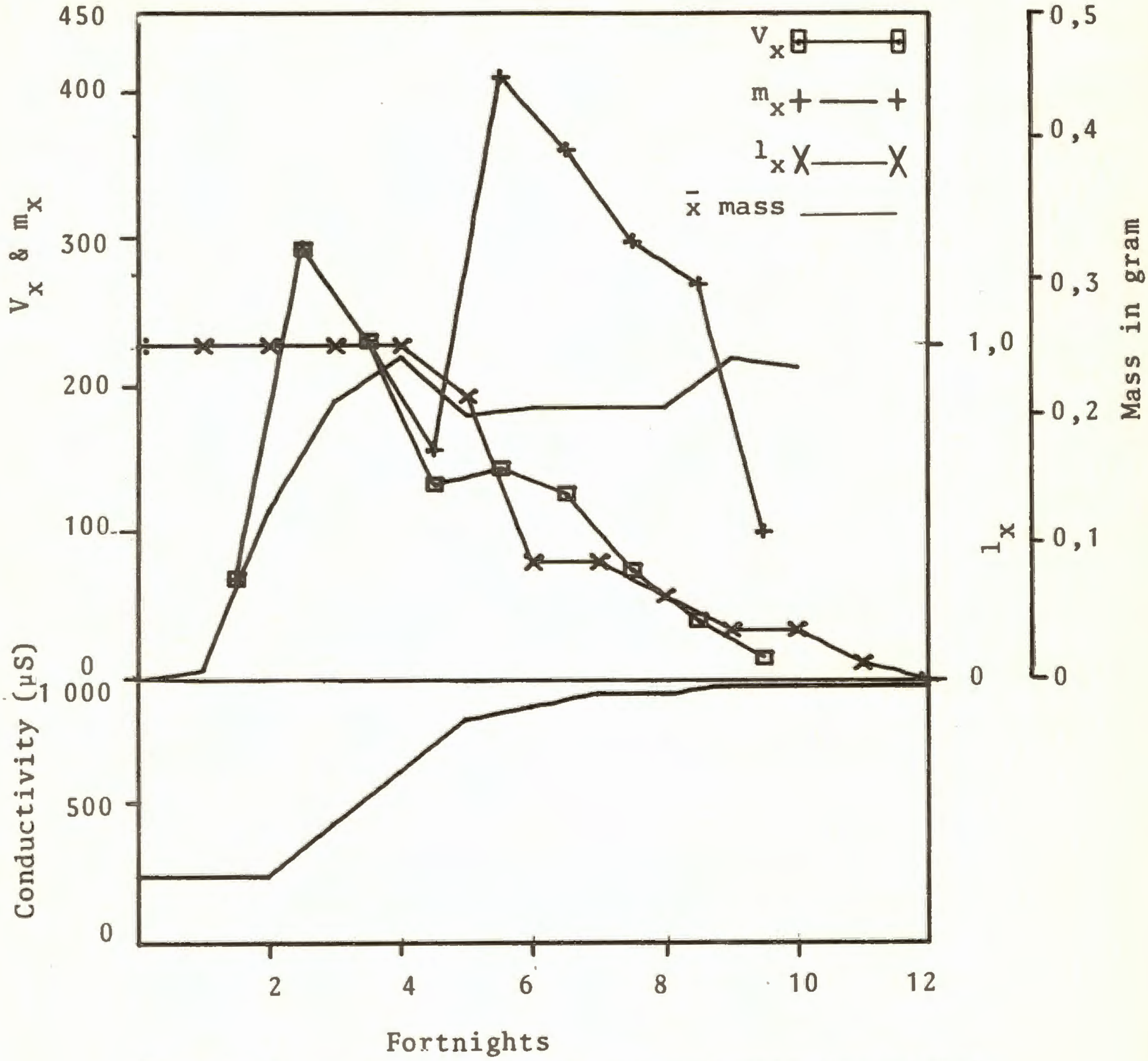


Figure 68. V_x, m_x, l_x values and mean fortnightly mass per snail of *B.(B.)tropicus* being subjected to a stepwise increase in con= ductivity

Table 47 : Population statistics of the snails being subjected to stepwise decreasing salinities.

	L.natalensis	*B.pfeifferi*	*B.(P.)globosus*	*B.(B.)tropicus*
Hatching time*	8	5	5	8
Hatching percentage	96,71	90,81	84,68	45,87
Start of egg production*	34	22	37	26
λ	7,3955	22,3894	5,8387	9,7972
r_m	2,0009	3,1086	1,7645	2,2821
r_c	1,5455	1,3628	1,1992	1,8082
R_o	1 081,700	3 162,790	1 371,933	989,2997
T_c	4,52038	5,9136	6,0239	3,8143

*In days

Table 48 : Population statistics of the snails being subjected to stepwise increasing salinities.

	L.natalensis	*B.pfeiferi*	*B.(P.)globosus*	*B.(B.)tropicus*
Hatching time*	10	11	11	8
Hatching percentage	96	90,86	85,69	69,68
Start of egg production*	30	19	31	20
λ	5,1711	39,5905	5,6564	19,1910
r_m	1,6431	3,6786	1,7328	2,9544
r_c	1,3358	1,7708	1,5173	1,5810
R_o	224,9000	1 614,9400	224,7500	1 134,3000
T_c	4,0543	4,1716	3,5687	4,4488

*In days

findings in the life table experiments. The rise in conductivity, however, had no effect on the mean individual egg production per fortnight as is evidenced by the m_x values.

Throughout the first four fortnights the growth rate of the cohort at 250 –> 1 000 µS was comparable to those of the other cohorts of *B.(B.) tropicus* but, as the conductivity was increased the growth rate dropped (appendix tables 21 and 26 and figure 68).

It is apparent that increasing and decreasing conductivities do not have the same effect on *B.(B.) tropicus*. Whereas the latter induces a drop in the egg production only, the former hardly affects egg production at all but has a very deleterious effect on survival.

A comparison of the effect of increasing salinity on the four species reveals only *B. pfeifferi* to be unaffected. Although the egg production of *B.(B.) tropicus* was not affected a sharp rise in mortalities occurred after the conductivity increased above 850 µS. *Lymnaea natalensis* and *B.(P.) globosus* were very nearly affected in the same way as can be seen by their drop in egg production and growth rates as the conductivity increased. Above 650 µS the mortality rate of the latter species also rose considerably.

3.9 Adaptation to salinity in two generations

It has been demonstrated by Watson (1953 and 1958) that *B.(B.) truncatus* is able to increase its tolerance towards salinity by a process of gradual acclimation. These observations are substantiated by Brumpt (1941) and Pimentel & White (1959) who found that *B. glabrata* could be changed from water with a low concentration of solids to one containing a high concentration by progressively acclimating the snails to the new water. Pimentel & White (1959) furthermore suggest that snails may be selectively bred to survive in waters with certain quantities of electrolytes. This implies that consecutive generations of certain individuals posess the ability to adapt to a changing environment.

During the previous experiments it was not possible to hatch *B. pfeifferi, B.(B.) tropicus* and *B.(P.) globosus* in water with a conductivity of less than 180 µS. The eggs of *L. natalensis* would not hatch at a conductivity lower than 125 µS or higher than 500 µS and *B. pfeifferi* and *B.(P.) globosus* could not be bred at conductivities higher than 750 µS.

There is a very significant difference between the snails used in the adaptation experiments and those used in the constant conductivity experiments which were discussed earlier on. In the case of the latter the parental snails consisted of unacclimatized, undomesticated wild stock and were maintained in the laboratory at a conductivity of 400 µS only for about one month by which time they had produced enough eggs to initiate the experiments. In the case of the former, however, eggs were obtained from two cohorts that had been kept at 180 µS and 750 µS respectively for one whole generation and which could, therefore, be regarded as acclimatized, domesticated stock which could possibly, to a certain extent, have become adapted to the two conductivities in question.

Another factor which should be considered when interpretating these results is the fact that the eggs used in the first series of experiments might have been unfavourably affected by their transfer from the 400 µS at which they were deposited to 180 and 750 µS which involved conductivity differences of 220 µS and 350 µS respectively. This difference was obviously very much smaller in the case of the adaptation experiments. The importance of this factor is, however, not easy to evaluate because it is generally not possible to completely isolate the role of any single factor in experiments such as these.

Eggs from the cohorts kept at 180 µS were transferred to water with a conductivity of 100 µS and the eggs from the cohorts at 750 µS to water with a conductivity of 900 µS. This involved conductivity changes of 80 µS and 150 µS respectively. The hatching percentages and growth and egg production rates were calculated for all cohorts which hatched successfully and commenced reproducing.

Life table of *B.(B.) tropicus* at 900 µS

All eggs hatched within eight days and this offspring started producing eggs 23 days after hatching (table 49). As the purpose of this experiment and the following two were to test the possiblility of any adaptation to conductivity, the performances of these cohorts have to be compared both with those of their parents and those of the cohort at 875 µS (table 34) in the case of *B.(B.) tropicus*. Any improvement in their performance over those of the latter two cohorts might be regarded as indicative of the ability of the species to adapt to higher salinities in succeeding generations if the eggs are hatched and maintained at a higher conductivity than the parent stock.

This experiment was terminated after 14 weeks because it has been shown by Birch (1948), DeWitt (1954) and De Kock (1973) that practically no contribution is made to the value of r_m

Table 49 : Population statistics of test cohorts of *B.tropicus*, *B.pfeifferi* and *B.(P.)globosus* at 900µS.

	B.(B.)tropicus	*B.pfeifferi*	*B.(P.)globosus*
Hatching time*	8	10	10
Hatching percentage	100	100	20
Start of egg production*	23	21	39
λ	9,883	18,200	3,601
r_m	2,2908	2,9012	1,281
r_c	1,5407	1,945	1,155
R_o	1 509,75	616,75	346,35
T_c	4,751	3,302	5,064

*In days

after a certain minimum duration of the experiment. This period was shown by De Kock (1973) to be six weeks in the case of *B. pfeifferi* which should also be valid in the case of *B.(B.) tropicus*.

Only the hatching percentage of 100% could be construed as representing any improvement over the performance of the parental snails (tables 34 and 49). The failure of the F_2 snails to equal or improve on their parents performance was not completely unexpected in view of the fact that they were subjected to a much higher conductivity. The results could possibly have been different had the F_2 snails been bred at the same conductivity as their parents.

In contrast to the performance described above there was a definite improvement on the performance of the unacclimatized cohort at 875 µS. Although the F_2 snails did not yield such a high m_x value (table 50 and figure 69) as those at 875 µS did (table 32) they reached their highest value five fortnights earlier. As a result of their low mortality rate, the F_2 snails did, moreover, afford a V_x value which was so much higher than that of the cohort at 875 µS that, in spite of the fact that this experiment was only run for seven fortnights, it yielded a much higher net reproductive rate (R_o). The shorter pre-oviposition period combined with a lower T_c value and better reproductive and lower mortality rates were consequently responsible for the higher r_m recorded for the cohort of F_2 snails. The difference in growth rates between the two cohorts cannot, however, be regarded as being of any significance (appendix tables 21 and 25) because both were lower than the growth rate recorded for the cohort at 1 000 µS. Although the F_2 snails took longer to hatch they had a higher hatching percentage and a shorter pre-oviposition period than the snails at 875 µS (tables 49 and 34).

To be really significant, of course, the improved performance should be maintained through a longer series of F generations than the single one tested in the present study.

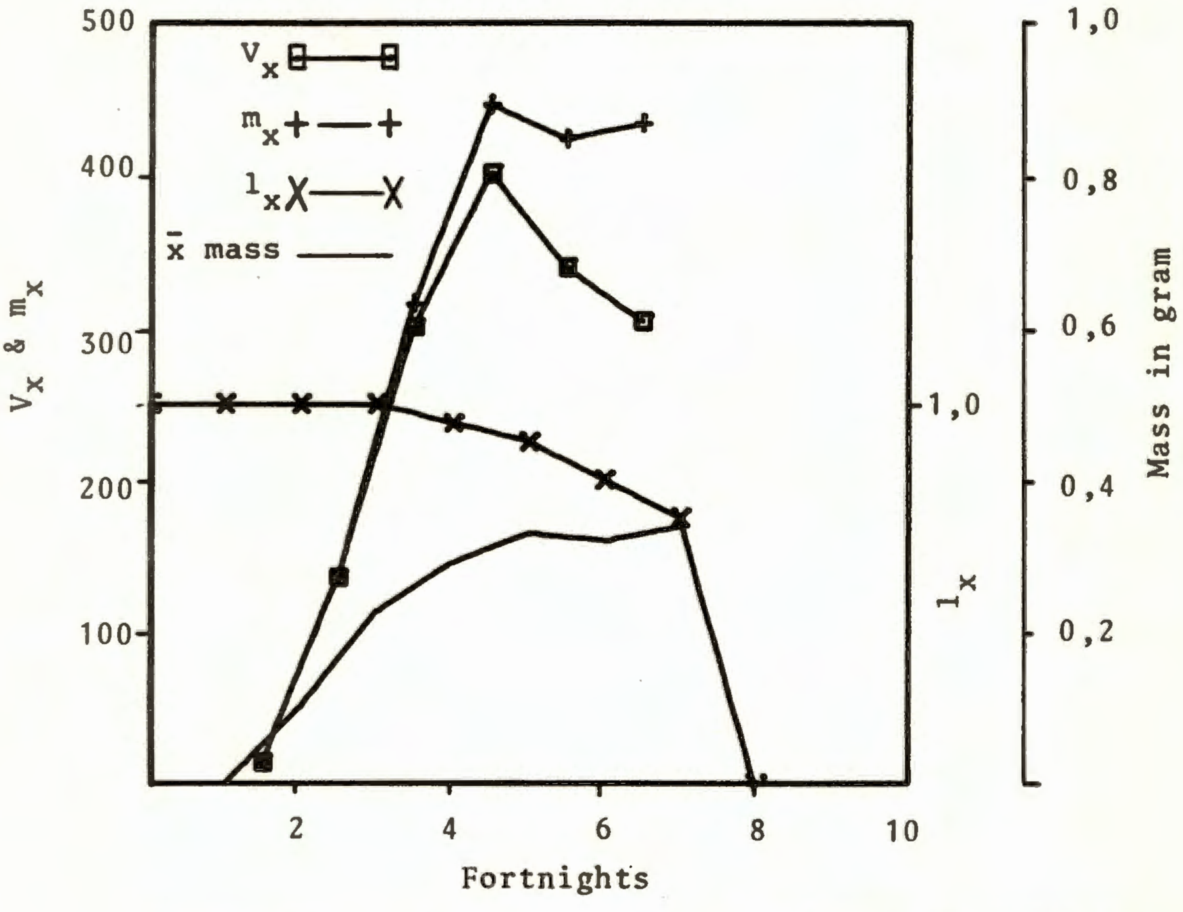


Figure 69. V_x, m_x, 1_x values and mean fortnightly mass per snail of the second (F_2) gene= ration of *B.(B.)tropicus.*

Table 50 : Life table of F_2 *B. (B.) tropicus.*

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	276	20	1,0000	13,8000	13,8000
2,5	2 716	20	1,0000	135,8000	135,8000
3,5	6 006	19	0,9500	316,1053	300,3000
4,5	8 031	18	0,9000	446,1667	401,5500
5,5	6 786	16	0,8000	424,1250	339,3000
6,5	6 080	14	0,7000	434,2857	304,0000

$R_o = \Sigma V_x = 1\ 509,7500$

Life table of *B. pfeifferi* at 900 μS

During both the present and a previous investigation (Jennings et al., 1973) attempts to breed unacclimatized specimens of *B. pfeifferi* at conductivities higher than 750 μS failed. In contrast to these findings 100% of the eggs of the acclimatized stock placed in water at 900 μS, hatched within ten days. Although these eggs, therefore, took two days longer to hatch than those at 750 μS the hatching percentage was higher. Moreover, the offspring produced their first eggs 21 days after hatching (table 49) which was ten days earlier than their parents did.

The F_2 cohort of acclimatized *B. pfeifferi* afforded a r_m of 2,9012 which was lower than the 3,1395 of the cohort at 750 μS. This was mainly the result of the lower reproduction and higher mortality rate of the F_2 cohort. A comparison of the growth rates also reflects an advantage for the cohort at 750 μS.

The m_x and V_x curves reached their highest values during the fourth fortnight (table 51 and figure 70). The first mortalities occurred after the third fortnight and during the seventh fortnight when the experiment was discontinued only four specimens had remained alive. However insignificant these findings might be, based, as they are, on one single generation, there can be little doubt that the eggs of *B. pfeifferi* specimens acclimatized at 750 μS did infinetely better at 900 μS than those of the unacclimatized specimens previously experimented with did at 875 μS.

Life table of *B.(P.) globosus* at 900 μS.

Although many more embryos developed within the capsules only 20% hatched successfully at this conductivity and the hatching time of 10 days was two days longer than the hatching time of the cohort at 750 μS. The pre-oviposition period of 39 days was also two days longer than that of the cohort at 750 μS (table

Table 51 : Life table of F_2 *B. pfeifferi.*

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	1 302	20	1,0000	65,1000	65,1000
2,5	4 308	20	1,0000	215,4000	215,4000
3,5	4 380	19	0,9500	230,5263	219,0000
4,5	1 176	14	0,7000	84,0000	58,8000
5,5	509	5	0,2500	101,8000	25,4500
6,5	360	4	0,2000	90,0000	18,0000

$R_o = \Sigma V_x = 616,7500$

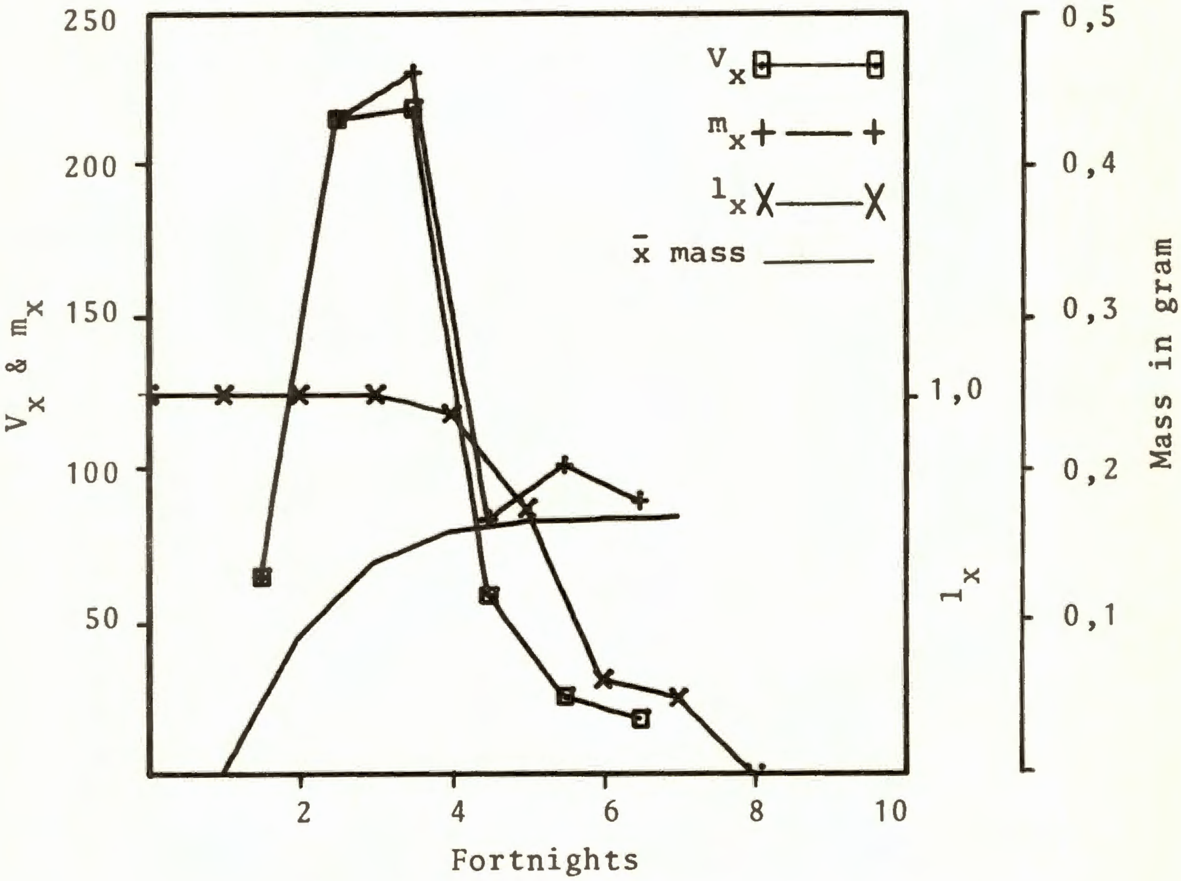


Figure 70. V_x, m_x, l_x values and mean fortnightly mass per snail of the second (F_2) generation of *B.pfeifferi*.

49). The fecundity and egg curves reached their peaks during the fifth fortnight (figure 71 and table 52).

According to the data in tables 52 and figure 71 this cohort performed slightly better than the one at 750 μS (table 10) and the slight advantage enjoyed by the former was chiefly the result of a slightly higher reproductive rate during the first two reproductive fortnights (tables 49 and 10). The growth rate, however, of the F_2 cohort of *B.(P.) globosus* was considerably lower than that of their parents (appendix tables 12 and 25). By and large, therefore, *B.(P.) globosus* reacted less favourably to the present attempt at acclimatization than did either *B.(B.) tropicus* or *B. pfeifferi.*

At 100 μS attempts to breed F_2 *B.(B.) tropicus*, F_2 *B.(P.) globosus*, F_2 *B. pfeifferi* and F_2 *L. natalensis* failed. Only 20% of the *B.(B.) tropicus* eggs hatched while 94% and 95% of the *B. pfeifferi* and *B.(P.) globosus* eggs hatched respectively. Although the embryonal development of the *L. natalensis* eggs appeared to be quite normal they failed to escape from the capsules and died after a while. The hatchlings of the other three species described above, all died within a day or two of hatching Where it had thus been possible to breed F_2 *B. pfeifferi* and F_2 *B.(P.) globosus* at a higher conductivity than previously, attempts to breed them and F_2 *B.(B.) tropicus* and F_2 *L. natalensis* at a lower conductivity than previously failed.

It has been established by Brumpt (1941) that adult *B. glabrata* can adapt to changing salinities and similar adaptation has been described for *B. (B.) truncatus* by Watson (1953 and 1958). This adaptation required a transitional period during which salinities were gradually changed, thereby allowing the snails to become acclimated. Information regarding adaptation by successive generations to changing salinities is, however, very meagre. In this respect, as has previously been mentioned, Pimentel & White (1959) state that snails may be selectively bred to survive in waters with a certain quantity of

Table 52 : Life table of F_2 *B. (P.) globosus*.

Pivotal age	Tot. egg production	No. of snails	Survival l_x	Fecundity m_x	$(l_x m_x)$ V_x
0,5	0	20	1,0000	0	0
1,5	0	20	1,0000	0	0
2,5	0	15	0,7500	0	0
3,5	744	15	0,7500	49,6000	37,2000
4,5	3 008	15	0,7500	200,5333	150,4000
5,5	2 352	15	0,7500	156,8000	117,6000
6,5	451	15	0,7500	30,0667	22,5500
7,5	92	11	0,5500	8,3636	4,6000

$R_o = \Sigma V_x = 346{,}3500$

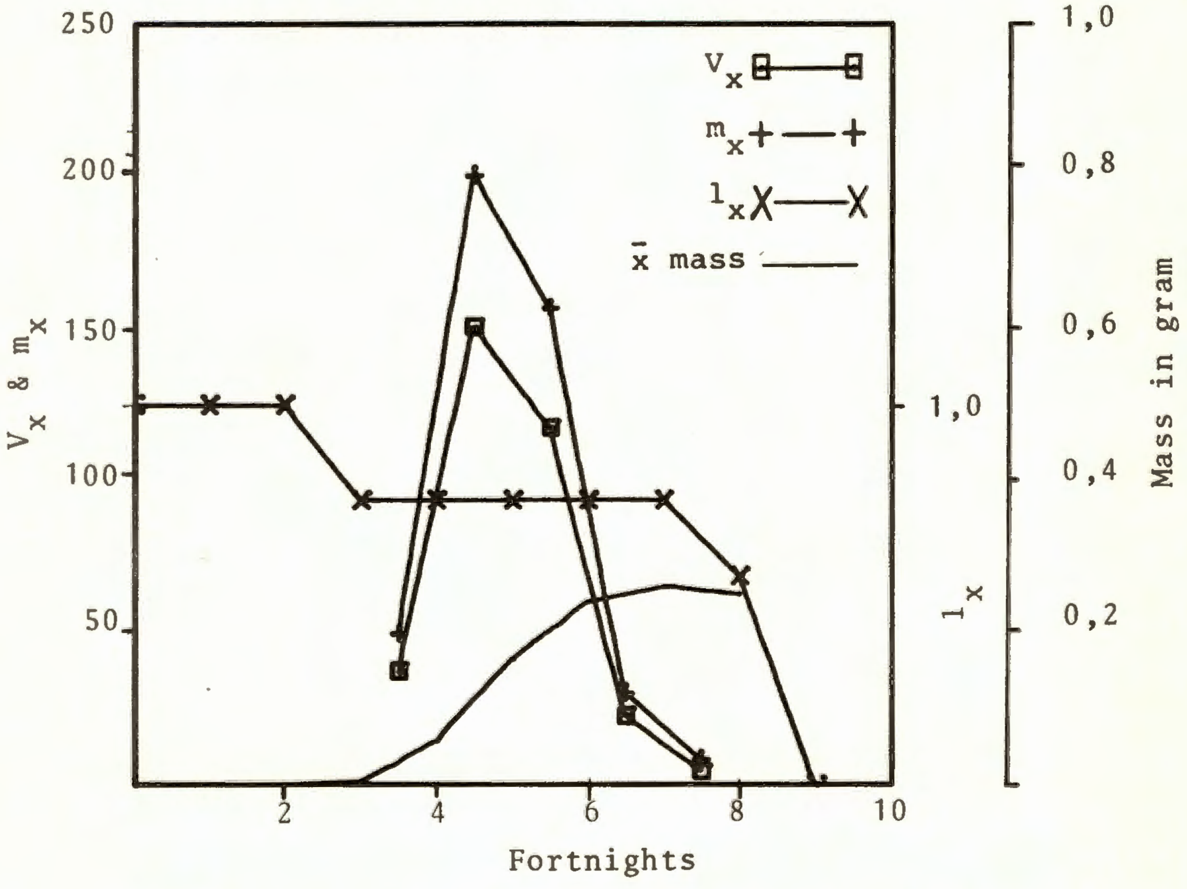


Figure 71. V_x, m_x, l_x values and mean fortnightly mass per snail of the second (F_2) generation of *B.(P.)globosus*

electrolytes. This theory seems to be substantiated by the results obtained in the present experiment in which it was possible to breed both *B. pfeifferi* and *B. (P.) globosus* at a conductivity (900 µS) at which previous breeding attempts had failed. The only significant difference between the two sets of eggs used was that one was laid by snails maintained for one generation in water with a much higher conductivity (750 µS) than the other (900 µS). The former hatched successfully at 900 µS whereas the latter failed to hatch at 875 µS.

Judging from these results it seems as if at least in the laboratory, successive generations could be adapted to changing quantities of electrolytes by selective breeding procedures and it is not unlikely that processes analogous to these might be in operation in the natural habitats.

3.10 Interspecies comparison

125 µS

Bulinus (P.) globosus exhibited the highest hatching percentage and shortest hatching time of the species tested at this conductivity while *L. natalensis* was second as regards hatching percentage (tables 10, 18, 24 and 34). Both *B.(B.) tropicus* and *B. pfeifferi* attained hatching percentages of 13% but the latter's hatching time was exceptionally long. Judging from these two statistics *B.(P.) globosus* might be considered to be best capable of tolerating this low conductivity. However, although only a couple of hatchlings of *L. natalensis* managed to survive for longer than a few days and although their performance at this conductivity was much lower than that at any of the other conductivities, the fact that they were able to survive and reproduce at this conductivity indicates that this species enjoys a definite advantage over the other three at low conductivities.

The death of hatchlings so soon after birth indicates that not even the minimum requirements of these snails in respect of certain ions were met and it is not impossible that in water with the same conductivity but with a different ionic composition survival might be unaffected.

180 µS

Hatching times of six, seven, eight and 10 days were recorded for *B.(B.) tropicus*, *B.(P.) globosus*, *B. pfeifferi* and *L. natalensis* respectively and the latter two species gave the highest hatching percentages. The lowest hatching percentage of 55,05%, recorded for *B.(B.) tropicus* was only 12,91% lower than than for *B.(P.) globosus* (table 53).

Table 53

Population statistics at 180 µS

	B.pfeifferi	*L.natalensis*	*B.(P.)globosus*	*B.(B.)tropicus*
Hatching time*	8	10	7	6
Hatching percentage	95	94,91	67,96	55,05
Pre-oviposition period*	26	37	48	28
λ	12,646	4,668	2,633	5,807
r_m	2,5373	1,5407	0,9679	1,7590
R_o	2 966,85	815,75	518,30	538,65
T_c	6,713	5,236	7,873	5,164

* In days.

The best survival rate (1_x) was achieved by *B. pfeifferi* (figure 72) and the poorest by *L. natalensis*. Although *B.(B.) tropicus* suffered a high initial mortality it nevertheless survived longer than did *L. natalensis* although it was inferior to *B.(P.) globosus*.

Low mortalities combined with a high reproductive rate were responsible for the high net reproductive rate (R_o) of *B. pfeifferi* (figure 73). Although *L. natalensis* achieved a higher R_o value than did *B.(B.) tropicus* the latter had a higher initial reproductive rate and also a shorter period between hatching and the onset of oviposition. The lowerst R_o value was recorded for *B.(P.) globosus* which also took the longest to start producing eggs.

Although *B. pfeifferi* had the second highest T_c value, the high R_o value and short period between hatching and oviposition ensured that r_m was higher for this than for any of the other species bred at 180 µS (table 53). In spite of the fact that *L. natalensis* had a higher R_o than *B.(B.) tropicus* the latter afforded the higher r_m value mainly because of its higher initial reproductive rate and shorter pre-oviposition period.

All λ values were higher than one, indicating that all four species were capable of multiplying at 180 µS but with its λ value of 12,646 it is clear that *B. pfeifferi* was the most successful species at this conductivity.

250 µS

B.(B.) tropicus and *B. pfeifferi* both hatched within seven days, one day earlier than *B.(P.) globosus* and three days earlier than *L. natalensis* (table 54) but the latter gave the highest hatching percentage.

At this conductivity *B.(B.) tropicus* survived the longest in spite of a slightly higher mortality rate (figure 74) than the other three species. Both *B. pfeifferi* and *B.(P.) globosus* survived for exactly the same time and *L. natalensis* was the most short lived.

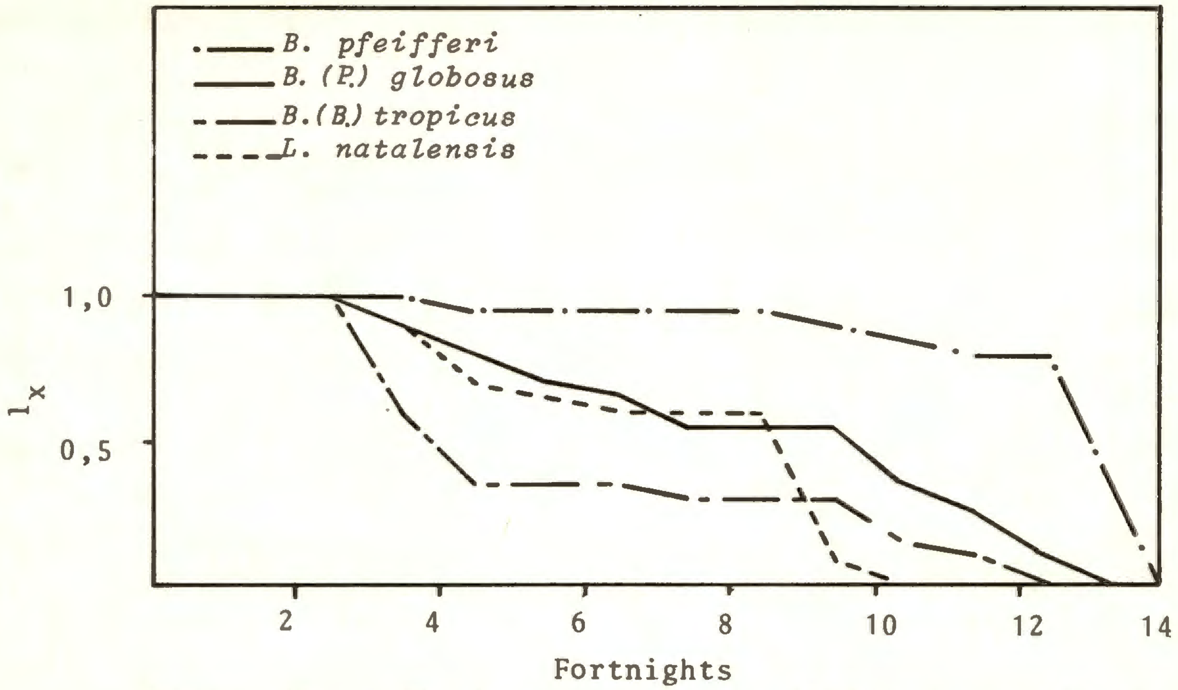


Figure 72. The 1_x curves of the different species at a conductivity of 180 μS

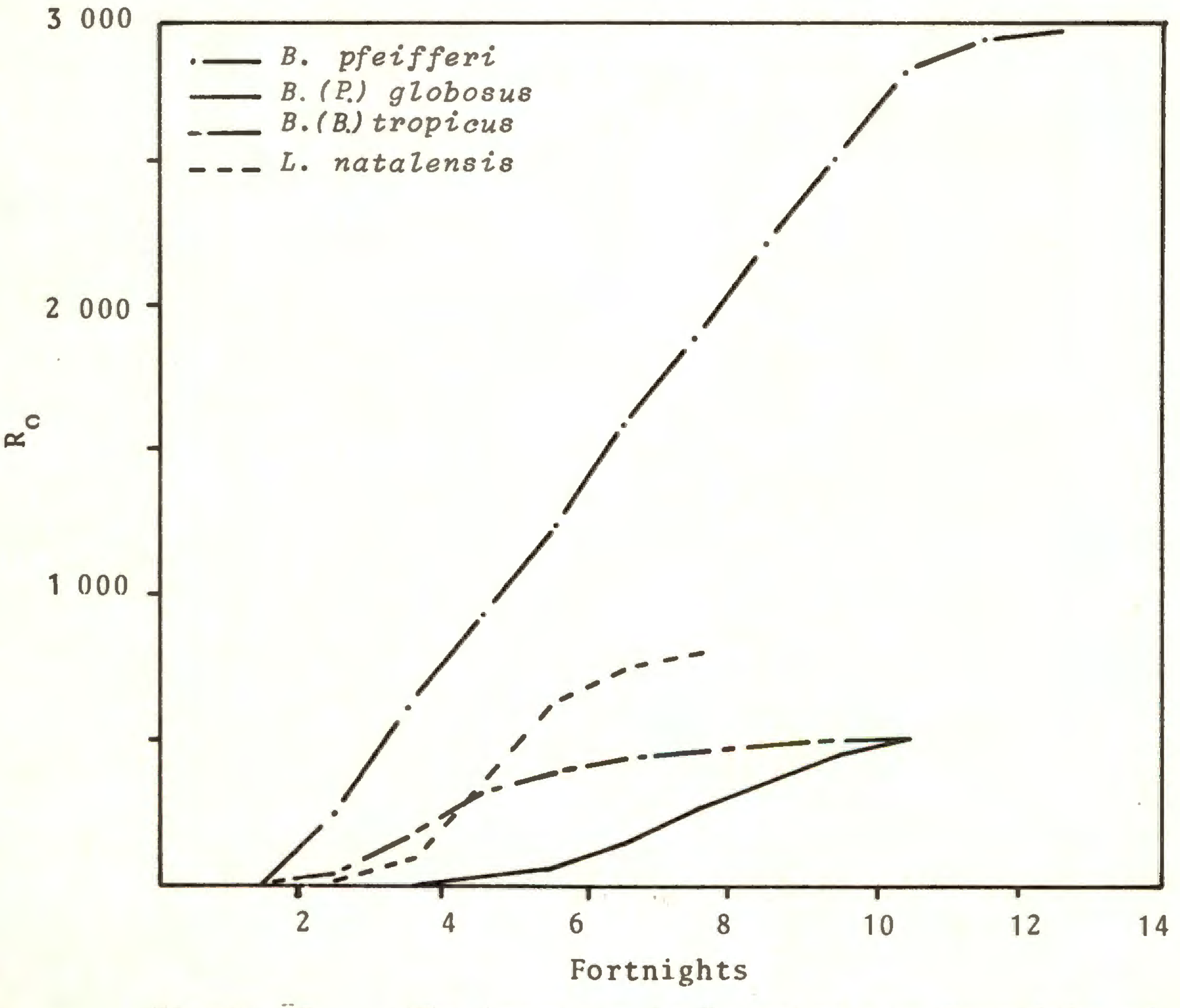


Figure 73. The increase in R_o value per fortnight of the different species at a conductivity of 180 μS

Table 54

Population statistics at 250 μS

	B.pfeifferi	*L.natalensis*	*B.(P.)globosus*	*B.(B.)tropicus*
Hatching time*	7	10	8	7
Hatching per=centage	86,8	95,70	82,18	70,27
Pre-oviposi=tion period*	20	25	43	20
λ	26,958	8,464	4,027	19,714
r_m	3,2943	2,1358	1,3929	2,9813
R_o	2 269,95	1 621,95	699,35	1 312,55
T_c	4,515	4,462	5,345	4,007

* In days.

B. pfeifferi not only achieved the highest reproductive rate but also the highest net reproductive rate (R_o) (figure 75). Although *B.(B.) tropicus* had a higher reproductive rate initially than did *L. natalensis* the latter overtook it and not only ended up with a higher reproductive rate but also a higher net repro=ductive rate (R_o). Both the lowest reproductive rate and net reproductive rate (R_o) were recorded for *B. globosus*.

As a result of its high net reproductive rate (R_o) and short pre-oviposition period *B. pfeifferi* yielded both the highest r_m and λ values. Its T_c value, however, was longer than that of *B. tropicus*. Its λ value of 26,958 was the best calculated for *B. pfeifferi* at all the conductivities excluding 375 μS where it was 28,285.

310 μS

With hatching times of seven days both *B.(B.) tropicus* and *L. natalensis* hatched the earliest while both *B.(P.) globosus* and *B. pfeifferi* took nine days to hatch (table 55). The hatching

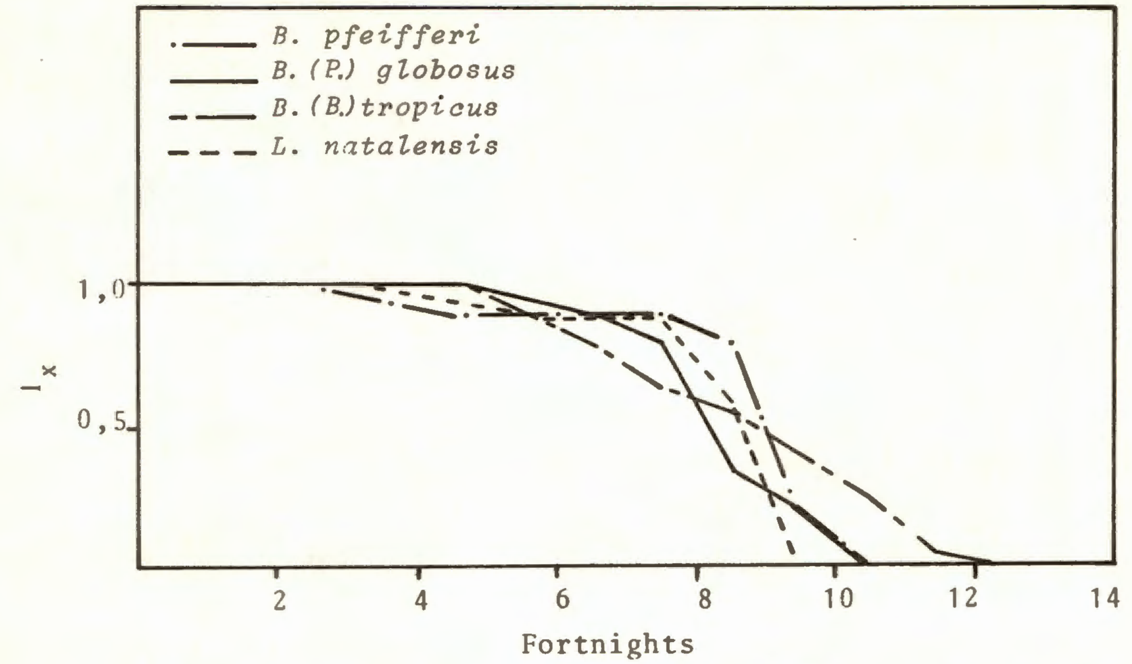


Figure 74. The l_x curves of the different species at a conductivity of 250 µS

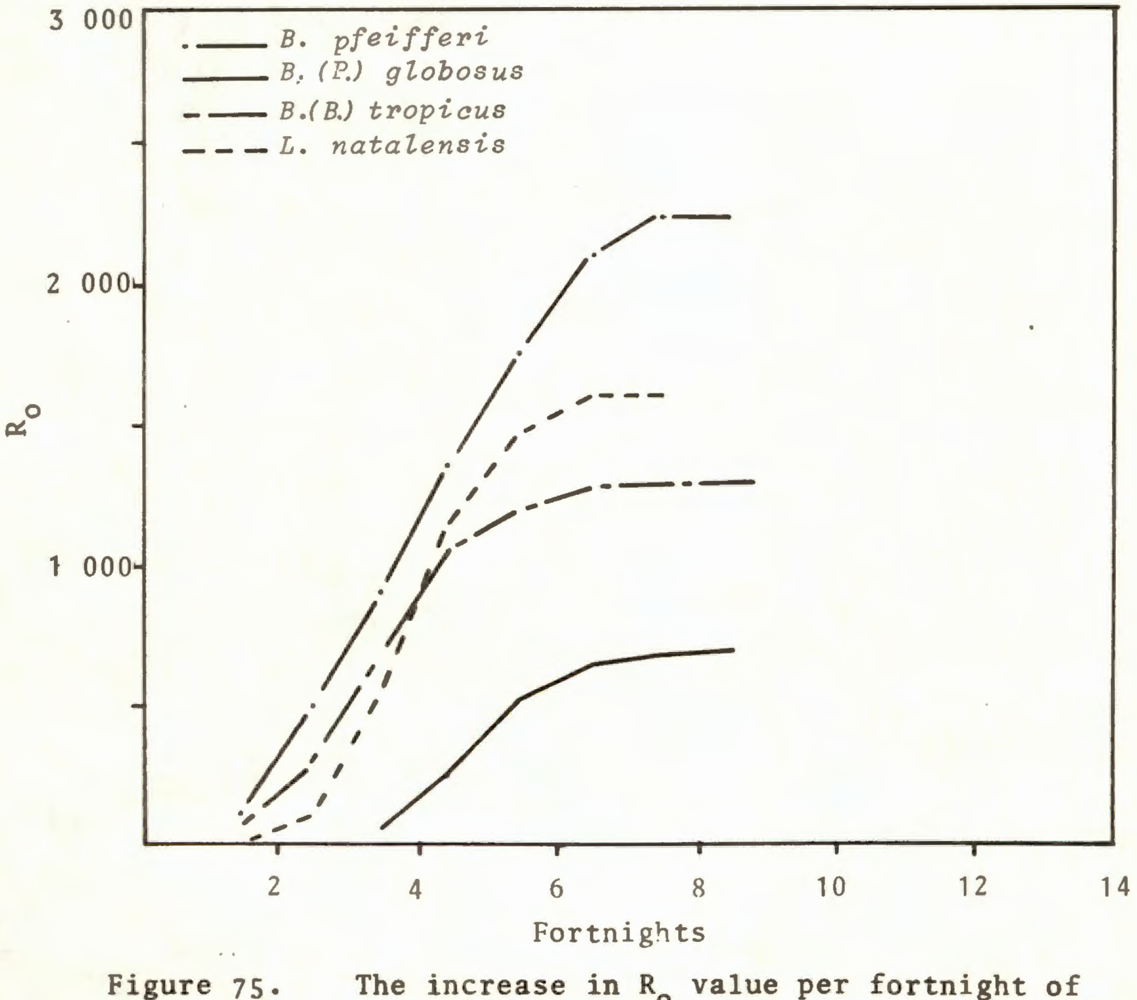


Figure 75. The increase in R_o value per fortnight of the different species at a conductivity of 250 µS

percentage sequence was *B. pfeifferi* > *L. natalensis* > *B. tropicus* > *B.(P.) globosus*. The hatching percentage of 44% recorded for the latter is, however, regarded as being abnormally low since at conductivities both preceding (250 µS) and succeeding (375 µS) it in the conductivity sequence higher values for this factor (table 10) were recorded.

Table 55

Population statistics at 310 µS

	B.pfeifferi	*L.natalensis*	*B.(P.)globosus*	*B.(B.)tropicus*
Hatching time*	9	7	9	7
Hatching percentage	91,7	88,10	44	60,61
Pre-oviposition period *	21	31	28	35
λ	17,824	4,634	6,585	4,832
r_m	2,8806	1,5335	1,8848	1,5752
R_o	1 189,50	482,65	1 372,55	684,00
T_c	3,809	4,693	5,813	5,809

*In days

Although mortalities started earliest in the cohort of *B.(P.) globosus*, this cohort managed to survive longest (figure 76). A high mortality rate after the sixth fortnight caused *B. pfeifferi* to survive shortest.

As a result of a long survival period and reasonably substantial egg production *B.(P.) globosus* yielded the highest R_o value despite a lower reproductive rate and longer pre-oviposition period than was registered for *B. pfeifferi* (figure 77). This conductivity was calculated to be very close to the optimum required for the breeding of *B.(P.) globosus*.

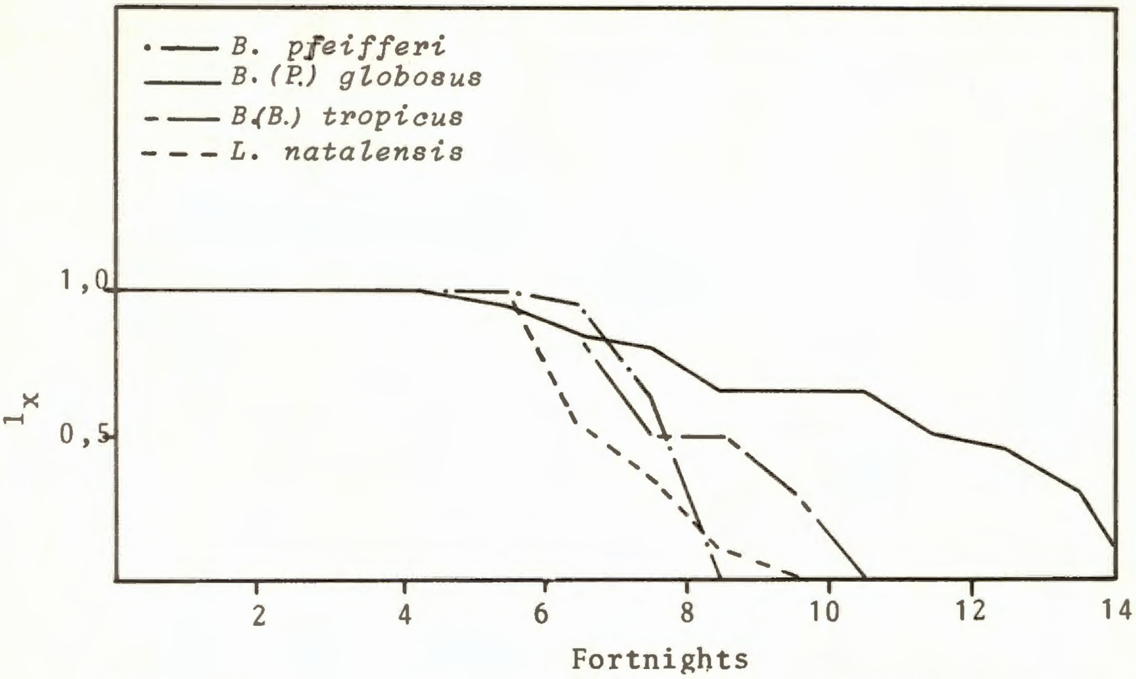


Figure 76. The 1_x curves of the different species at a conductivity of 310 μS

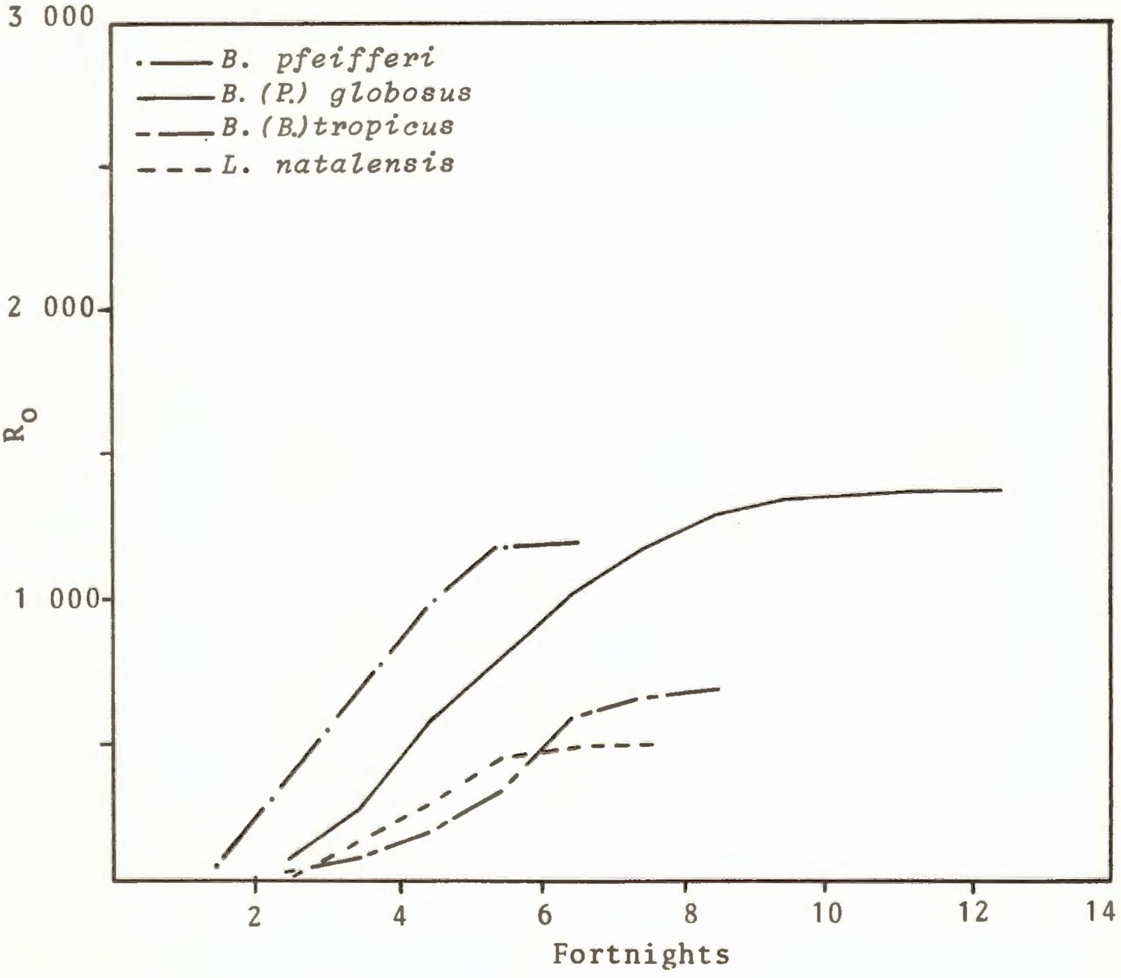


Figure 77. The increase in R_o value per fortnight of the different species at a conductivity of 310 μS

All r_m values were positive and the λ values were all higher than one, indicating the suitability of this conductivity for these four species.

375 μS

The hatching time sequence was as follows: *B.(B.) tropicus* < *B. pfeifferi* < *B.(P.) globosus* < *L. natalensis* (table 56) but the highest hatching percentage was recorded for *B. pfeifferi* with *B.(P.) globosus* and *L. natalensis* very close to each other in this respect.

Biomphalaria pfeifferi showed a very high hatching percentage at this conductivity and although the eggs hatched one day later than those of *B.(B.) tropicus*, its pre-oviposition period was also shorter than those of the three other species.

Table 56

Population statistics of the four species at 375 μS

	B.pfeifferi	*L.natalensis*	*B(P.)globosus*	*B.(B.)tropicus*
Hatching time*	7	10	8	6
Hatching per= centage	98,6	81,08	84,76	66,67
Pre-oviposi= tion period*	20	32	31	21
λ	28,285	5,924	6,361	11,154
r_m	3,3423	1,7791	1,8502	2,412
R_o	409,90	330,15	261,40	372,45
T_c	2,258	3,614	3,414	3,160

* In days

These statistics for *L. natalensis* and *B.(P.) globosus* were very similar at this conductivity and only the hatching times differed by two days.

The very short survival period of all four species at this conductivity has been discussed previously and is quite obvious from the 1_x curves in figure 78 which were drawn to the same scale as those for these species at the other conductivities. The short period during which they were able to produce eggs was the main reason for the very low R_o values recorded by all four species at 375 µS (figure 79). It is fortunate that the factor(s) responsible for the rapid increase in mortalities took effect only after sufficient reproductive fortnights had passed to enable an accurate calculation of the r_m value for each of these cohorts. It was at this conductivity that highest r_m and λ values were recorded for *B. pfeifferi*. From the values of these two statistics given in table 56 it is clear that all four species were able to survive and multiply at 375 µS without any obvious ill effects.

<u>500 µS</u>

Here 58,14% of the eggs of *L. natalensis* hatched within 12 days. Both these values, when compared to those at 310 µS and 375 µS, suggest that at 500 µS this species was approaching the upper limit of the tolerance to salinity and this was confirmed by the inability of the hatchlings to survive (table 24). The eggs of *B.(B.) tropicus* hatched within seven days which was one day earlier than those of either *B. pfeifferi* or *B.(P.) globosus*. For *B. pfeifferi*, however, the highest hatching percentage as well as the shortest pre-oviposition period was recorded (table 57).

Mortalities set in at least three fortnights earlier in the cohorts of *B.(P.) globosus* and *B.(B.) tropicus* than in those of *B. pfeifferi* (figure 80). In spite of this initial advantage the cohort of *B. pfeifferi* outlived the cohort of *B.(P.) globosus*

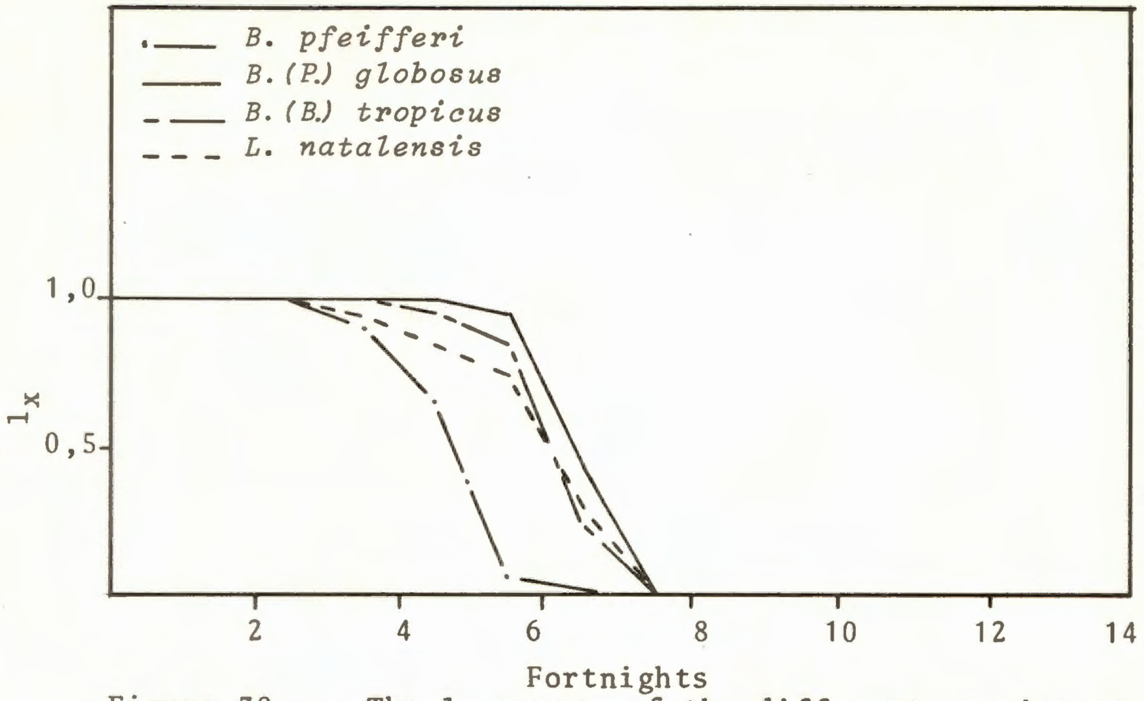


Figure 78. The 1_x curves of the different species at a conductivity of 375 µS

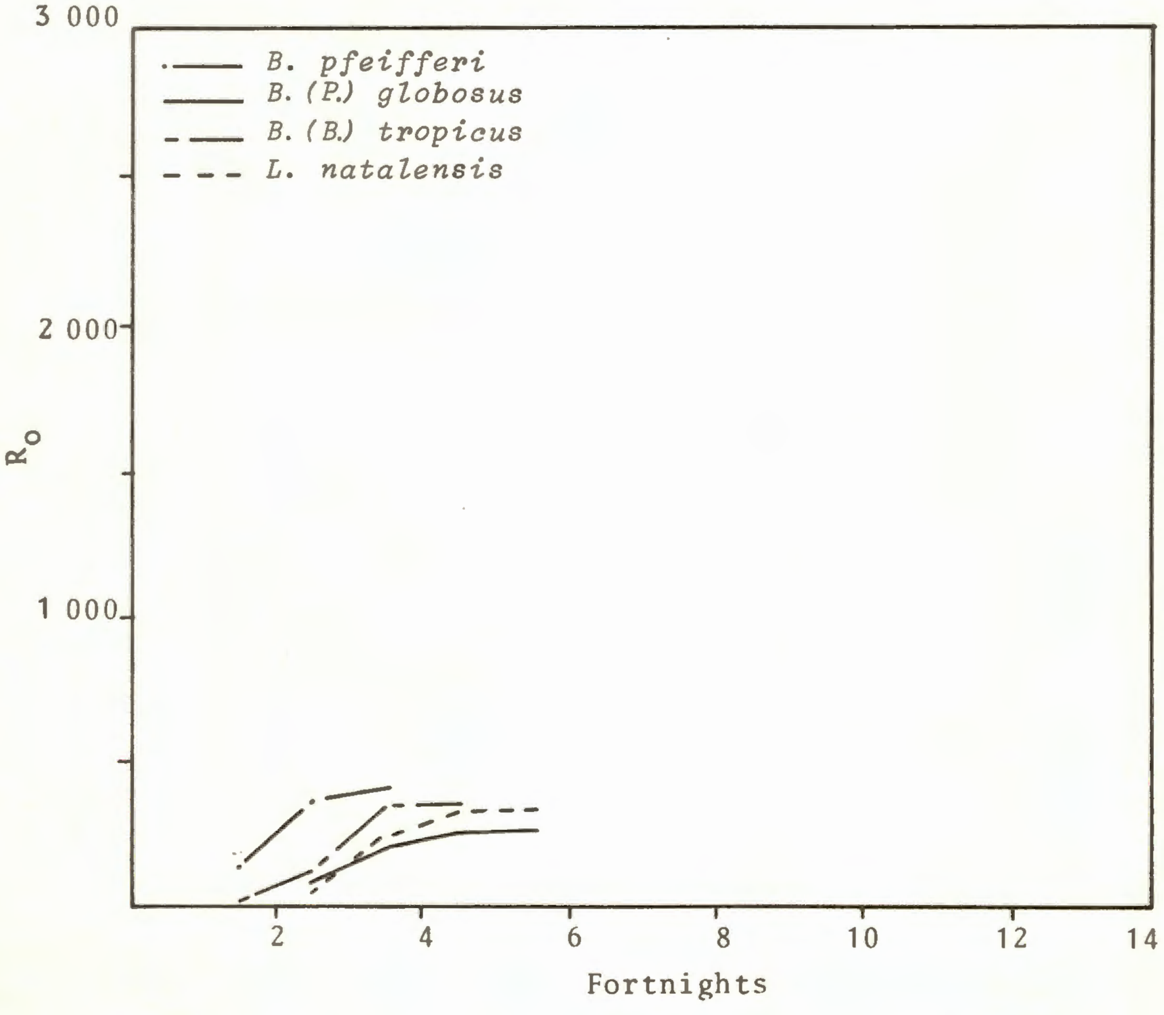


Figure 79. The increase in R_o value per fortnight of the different species at a conductivity of 375 µS

Table 57

Population statistics at 500 μS

	B.pfeifferi	*L.natalensis*	*B(P.)globosus*	*B.(B.)tropicus*
Hatching time*	8	12	8	7
Hatching percentage	93,1	58,14	83,33	78,94
Pre-oviposition period*	20		37	28
λ	25,222		6,534	5,254
r_m	3,2277		1,8770	1,6590
R_o	2 812,45		1 682,10	818,95
T_c	5,972		6,000	6,2000

*In days

by just one fortnight. *Bulinus (B.) tropicus* was the most short lived.

As *B. pfeifferi* maintained a higher reproductive rate throughout the experiment it also yielded the highest net reproductive rate (R_o) (figure 81). Although *B.(B.) tropicus* started producing eggs earlier than did *B.(P.) globosus* the latter achieved higher reproductive and net reproductive rates (table 57). As a result of having the highest R_o and the lowest T_c values *B. pfeifferi* gave the highest r_m and λ values.

625 μS

The eggs of *L. natalensis* were unable to hatch at this conductivity. The eggs of *B. pfeifferi* and *B.(P.) globosus* hatched within eight days and those of *B.(B.) tropicus* one day later (table 58). Very high hatching percentages were recorded for all three species but there was a definite delay in the onset of

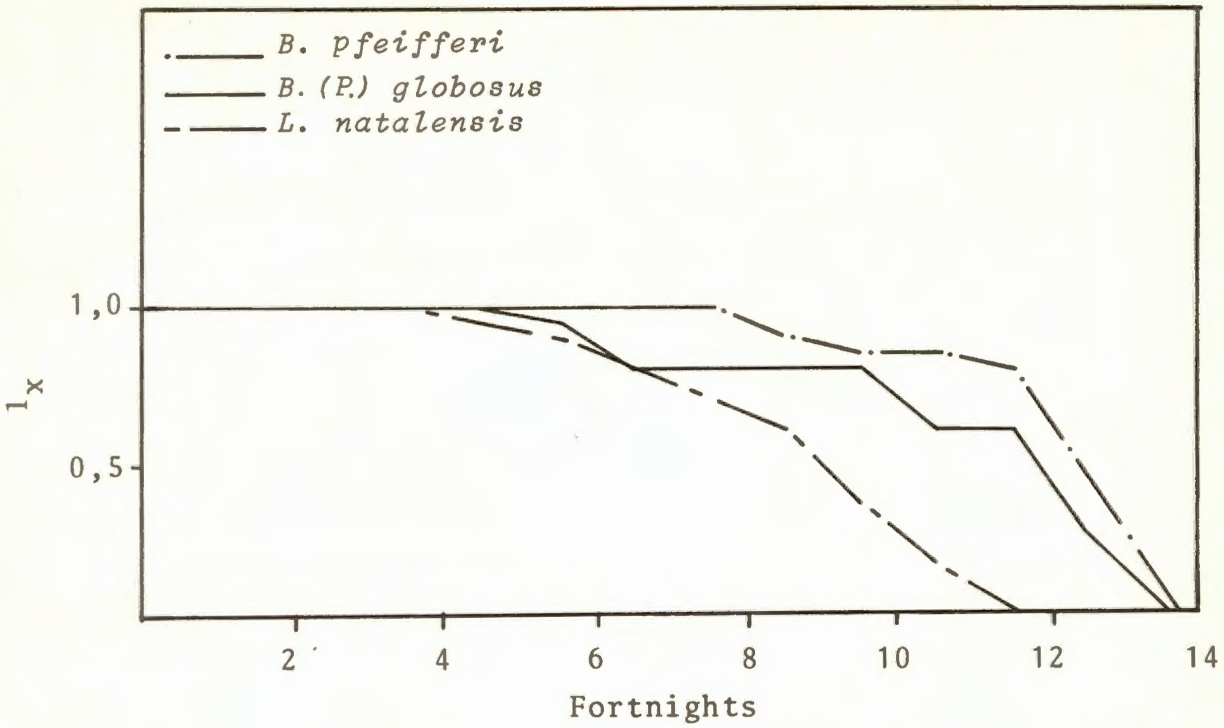


Figure 80. The l_x curves of the different species at a conductivity of 500 µS

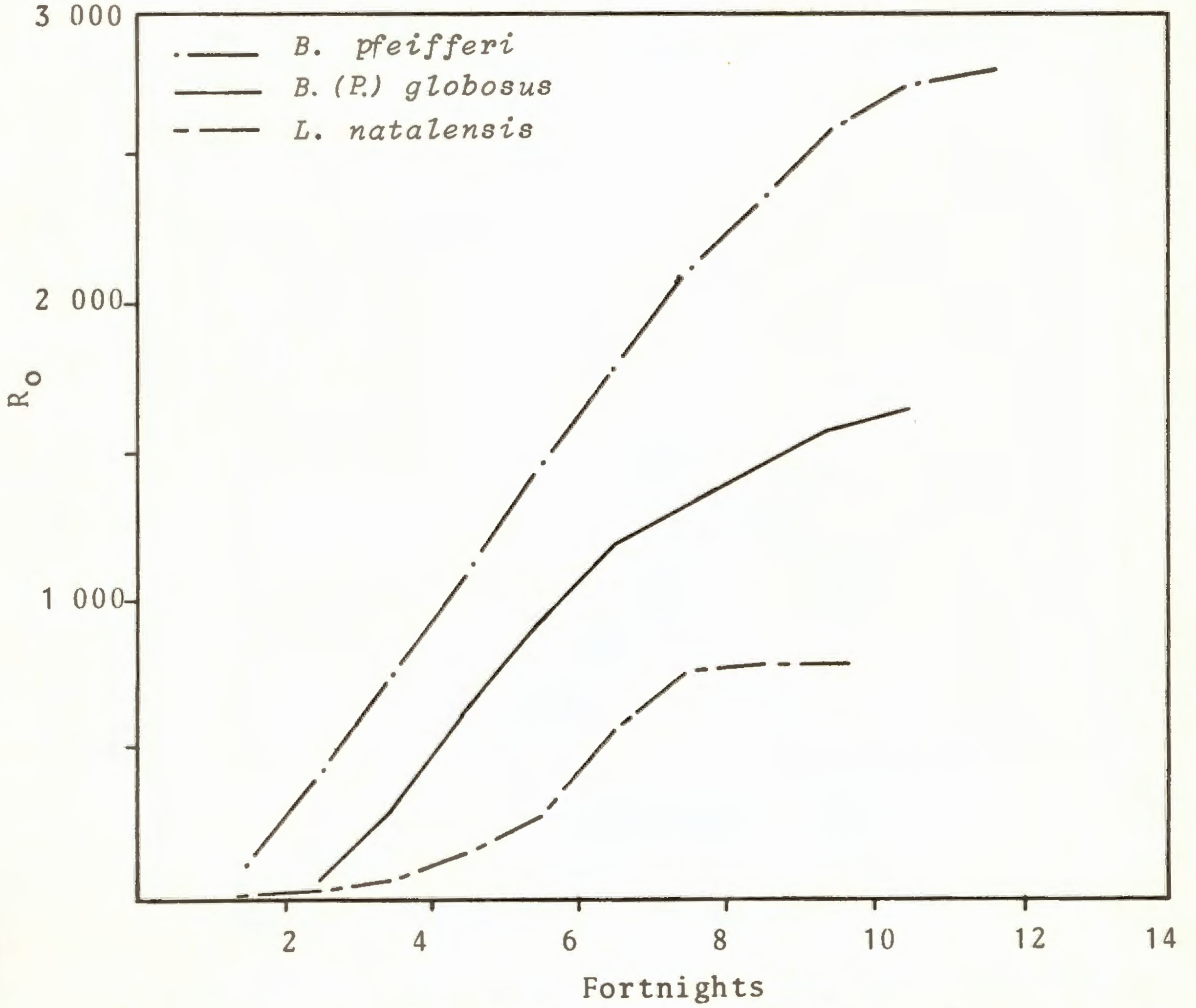


Figure 81. The increase in R_o value per fortnight of the different species at a conductivity

egg production in *B. pfeifferi* and *B.(P.) globosus*. In the latter's case the delay also occurred at 500 μS. (table 57). The period between hatching and oviposition of *B.(B.) tropicus* was 20 days and the r_m value of 2,6095 was the highest calculated for the species at any of the conductivities tested.

Although *B.(B.) tropicus* experienced an initially higher mortality rate and earlier mortality than the other two species, it survived one fortnight longer than both (figure 82). The mortality rates and survival periods of *B. pfeifferi* and *B.(P.) globosus* were practically the same.

Table 58

Population statistics at 625 μS

	B. pfeifferi	*B.(P.) globosus*	*B.(B.) tropicus*
Hatching time*	8	8	9
Hatching percentage	91,8	95,49	92,59
Pre-oviposition period*	31	37	20
λ	13,592	6,016	24,627
r_m	2,6095	1,7944	3,2038
R_o	1 622,55	1 061,50	2 378,00
T_c	5,097	5,075	4,800

*In days

The sequence for both net reproductive rate (R_o) and reproductive rate was *B. tropicus* > *B. pfeifferi* > *B.(P.) globosus* and this together with a low T_c value were responsible for the high and r_m values calculated for *B.(B.) tropicus* (figure 83).

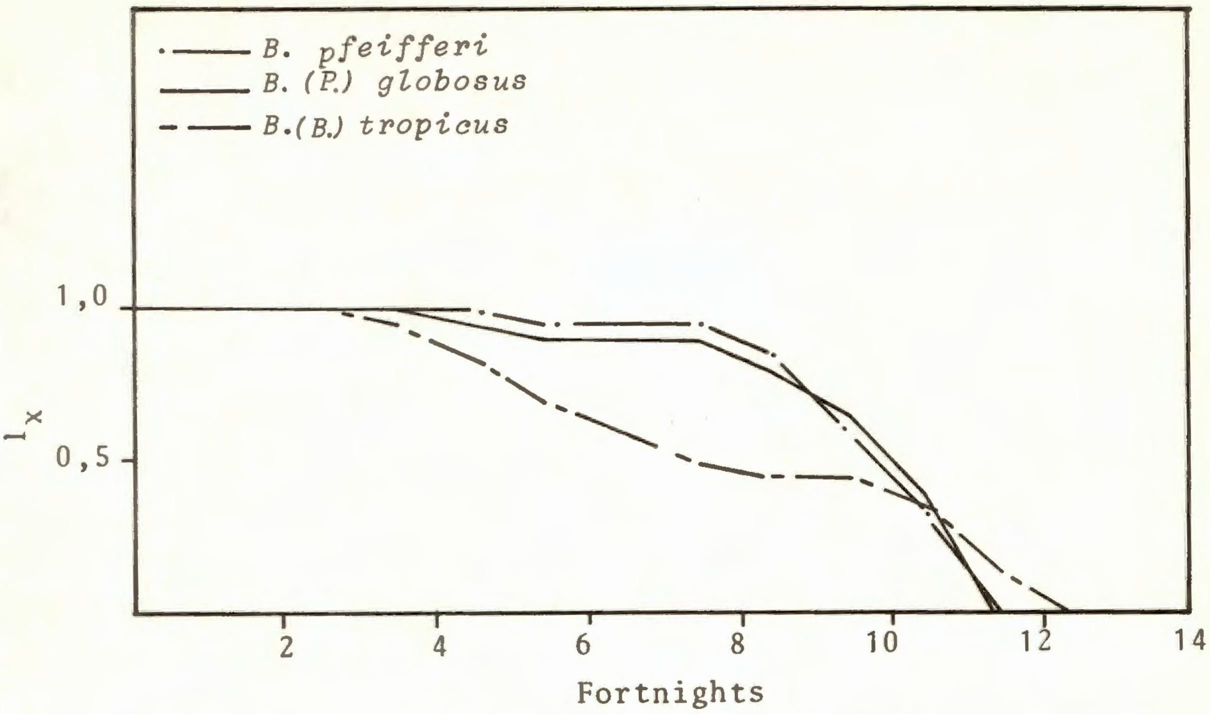


Figure 82. The l_x curves of the different species at a conductivity of 625 µS

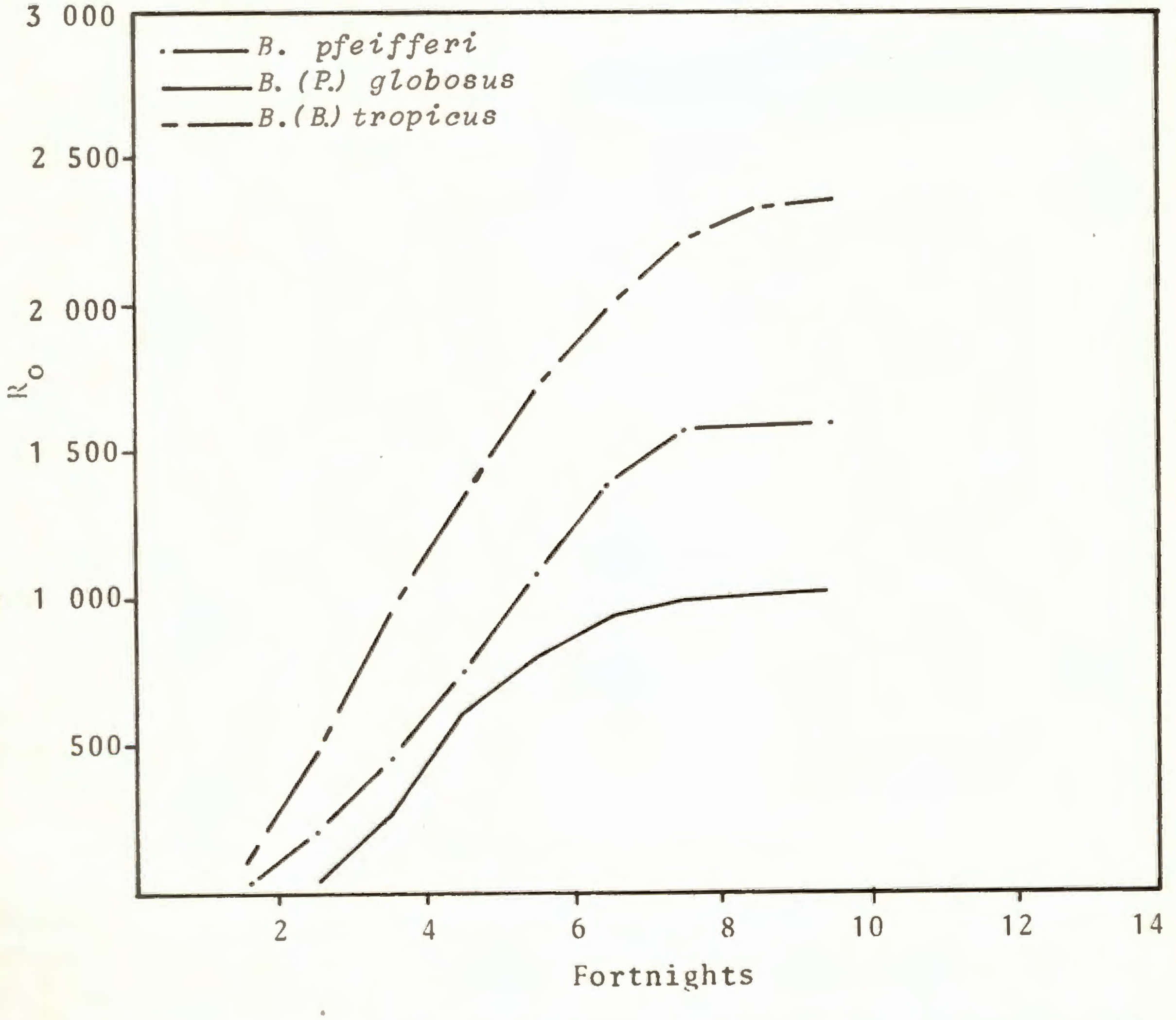


Figure 83. The increase in R_o value per fortnight of the different species at a conductivity of 625 µS

750 μS

This was the highest conductivity at which both *B.(P.) globosus* and *B. pfeifferi* could be bred. A characteristic of these high conductivities was the very high hatching percentages recorded for all the species (table 59) and in this case these values were practically identical for the three species. The delay in the onset of egg production that was already observed at 500 μS and 625 μS also occurred at 750 μS in the cases of both *B. pfeifferi* (not at 500 μS) and *B.(P.) globosus*.

Table 59

Population statistics at 750 μS

	B.pfeifferi	*B.(P.)globosus*	*B.(B.)tropicus*
Hatching time *	8	8	7
Hatching percen=tage	93,5	93,46	93,06
Pre-oviposition period	31	37	19
λ	23,093	3,557	16,673
r_m	3,1395	1,2689	2,8138
R_o	2 674,50	1 035,62	1 604,35
T_c	5,919	6,977	4,941

*In days

The cohorts of *B.(B.) tropicus* and *B.(P.) globosus* survived longest in spite of a high mortality rate exhibited by the former (figure 84). Except for the delay in the onset of egg production the high conductivity seemed to have no ill effect on the performance of *B. pfeifferi* and from figure 85 it can be seen that this species achieved both the highest reproductive and net reproductive rates. At this conductivity as well as at 625 μS it was obvious that conditions were not favourable

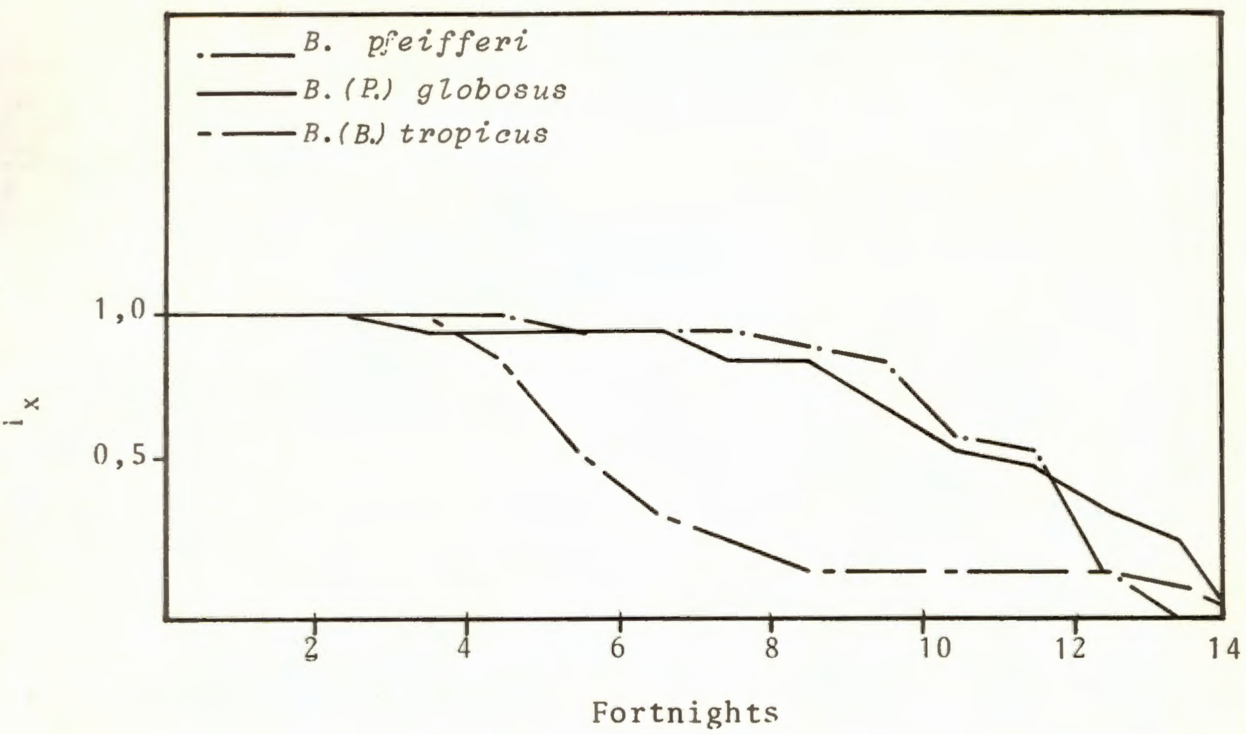


Figure 84. The l_x curves of the different species at a conductivity of 750 µS

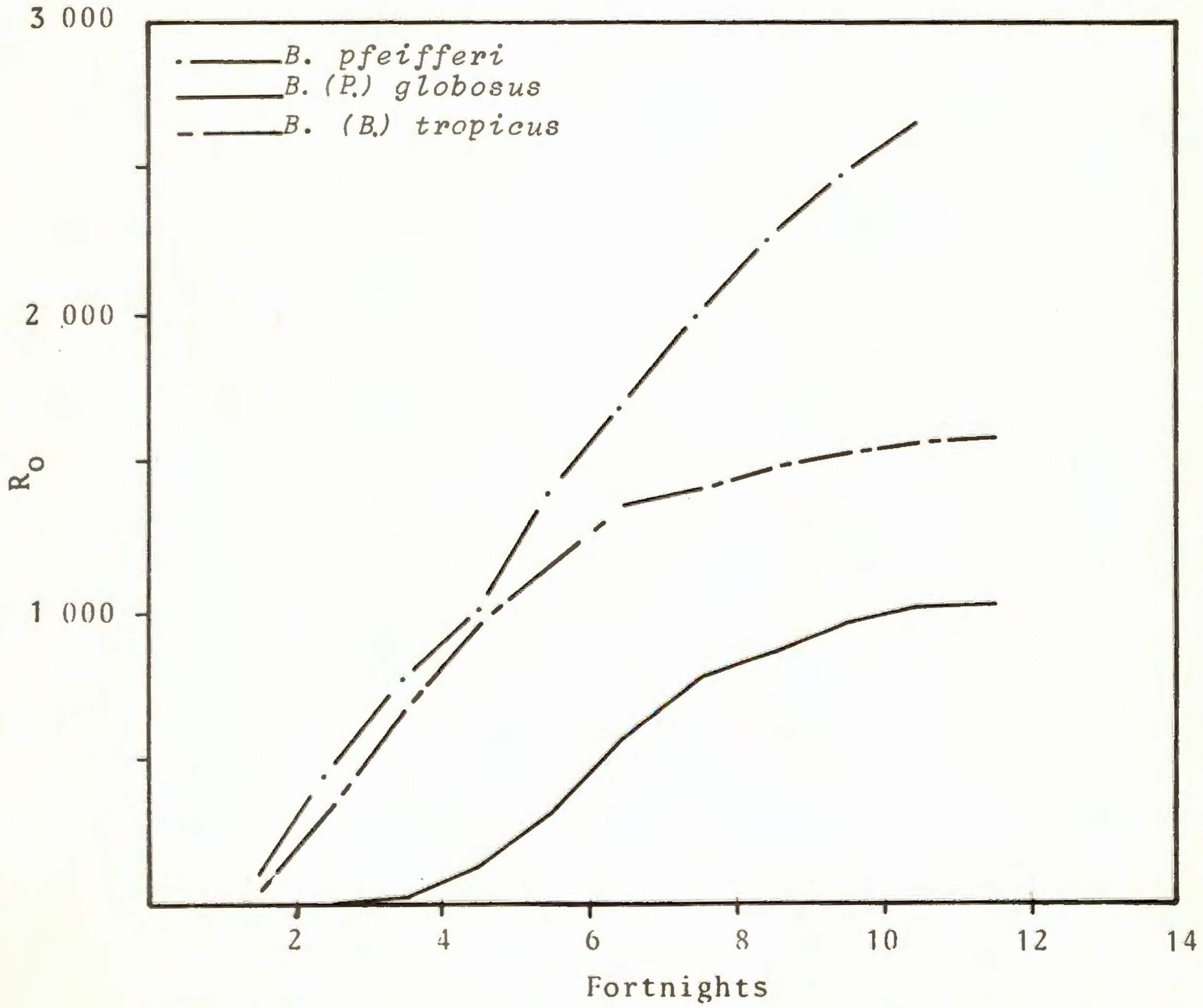


Figure 85. The increase in R_o value per fortnight of the different species at a conductivity

for *B.(P.) globosus* as there was a considerable decline in its performance, especially so at 750 µS. A similar reaction by this species was noted at 250 µS and 180 µS (table 10).

875 µS and 1 000 µS

Only *B.(B.) tropicus* could be bred at these conductivities and although hatching times and percentages were of the same order as those at the other conductivities a delay in the onset of ovi-position occurred (table 34). The values of the other statistics were not affected in any significant way except for the finite rate of increase (λ) which was lower than that of the cohorts at 625 µS and 750 µS.

A comparison of the R_0 curves in the preceding figures (figures 73, 75, 77, 79, 81, 83 and 85) shows that in only two instances, at conductivities of 310 µS and 625 µS, did *B. pfeifferi* fail to achieve the highest net reproductive rate of the four species tested. This is an indication of this species' ability to tolerate a wide range of salinities, a characteristic that gives *B. pfeifferi* an obvious advantage over the other three species in respect of habitat exploitation. In this respect *L. natalensis* which was severely affected by conductivities above 375 µS is at an obvious disadvantage.

From the discussion of the experiments designed to determine the adaptation to salinity in two generations (3.9) one might suspect that the eggs used in the constant conductivity experi=ments might, in certain cases, have been subjected to a conduc=tivity shock which could have affected the results obtained from these experiments. While the findings during the former experiments probably would not affect the general trend of the data obtained at the different constant conductivities analized above they may very well have a bearing on the actual values obtained for the different statistics recorded. As was brief=ly stated under 3.9 the eggs used in the constant conductivity experiments were obtainted from unacclimatized parent stocks maintained at 400 µS from which they were transferred to the different conductivities tested. In the cased of 50, 125, 180, 750, 875 and 1 000 µS, for example, this amounted to respective conductivity shocks of 350, 275, 220, 350, 475 and 600 µS. If a certain degree of adaptation to changing conductivities does in fact exist, as seems to be suggested by the data obtained for *B.(P.) globosus* and, to a greater extent, for *B. pfeifferi* and *B.(B.) tropicus* then the exact values recorded at the different constant conductivities might have been different had the parental stocks been acclimatized to higher or lower conductivities before experimenting with their offspring. This line of argument might be of special significance in the case of the values recorded for the cohorts at 375, 310 and 500 µS where the conductivity shocks were only 25,90 and 100 µS. Likewise in the case of the adaptation experiments the difference in conductivity between the water in which the parental snails were maintained and those of the waters to which their eggs were transferred was only 80 and 150 µS respectively. As a result of this conductivity shock it could, under certain conditions, be argued that the cohorts at the conductivities closer to that at which the parental stock had been kept, enjoyed an advantage over those cohorts at conductivities further away from this conductivity. This advantage, if indeed one existed, would mainly be manifested by improved values for those cohorts favoured by the lower conductivity shock, while the values for those cohorts penalized by the bigger conductivity shock would be lower than the ones actually obtained. It must, however, be emphasized once more that while a strong possibility of this having happened does exist, it is extremely improbable that the higher values that could be obtained by reducing the conductivity shock, would bring about any significant change in the general trend of the data obtained at the constant conductivities.

4. DISCUSSION AND CONCLUSIONS

At conductivities of 250 µS, 375 µS, 500 µS and 750 µS there was very little difference between the r_m values recorded for the cohorts of *B. pfeifferi* (table 20 and figure 86). Although the r_m values of the cohorts at 310 µS and 625 µS were much lower than those mentioned above, an overall pattern of practically equal performance at most conductivities tested can be discerned. At 180 µS the r_m value was low as a result of unfavourable con=ditions. The range of r_m values for *B. pfeifferi* in the present study was 0,8050 and is somewhat wider than the 0,6507 calcula=ted by Jennings et al. (1973) and the 0,4207 calculated by Williams (1970b) for the same species at various salinities. Although the absence of any single r_m value which was significantly higher than any of the others certainly reflects the insensitivity of *B. pfeifferi* to changes in the conductivity such as those to which it was subjected, the slightly higher r_m value recorded at 375 µS could be taken to indicate that this species might do better at conductivities in the region of 375 µS. This confirms the results of Jennings et al. (1973) who, after subjecting *B. pfeifferi* to very nearly the same range of conductivities as in the present study, concluded that this species shows a defini=te preference for waters with conductivities ranging from 300 µS to 400 µS.

Figure 87 represents a graphical presentation of the r_m values calculated for *B.(P.) globosus* at conductivities ranging from 180 µS to 750 µS. There were definite indications that on the basis of r_m values this species yielded its best results between 310 µS and 625 µS (table 10 and figure 87). Above and below these conductivities the r_m values were much lower. Although the r_m range for conductivities between 180 µS and 750 µS was 0,9169 that between 310 and 625 µS was only 0,0904, which indica=ted that between 310 and 625 µS conductivity had no marked effect and that *B.(P.) globosus* was sensitive only to conductivities above and below these levels. The positive r_m values calcula=ted at 180 µS, 250 µS and 750 µS, however, demonstrate that this

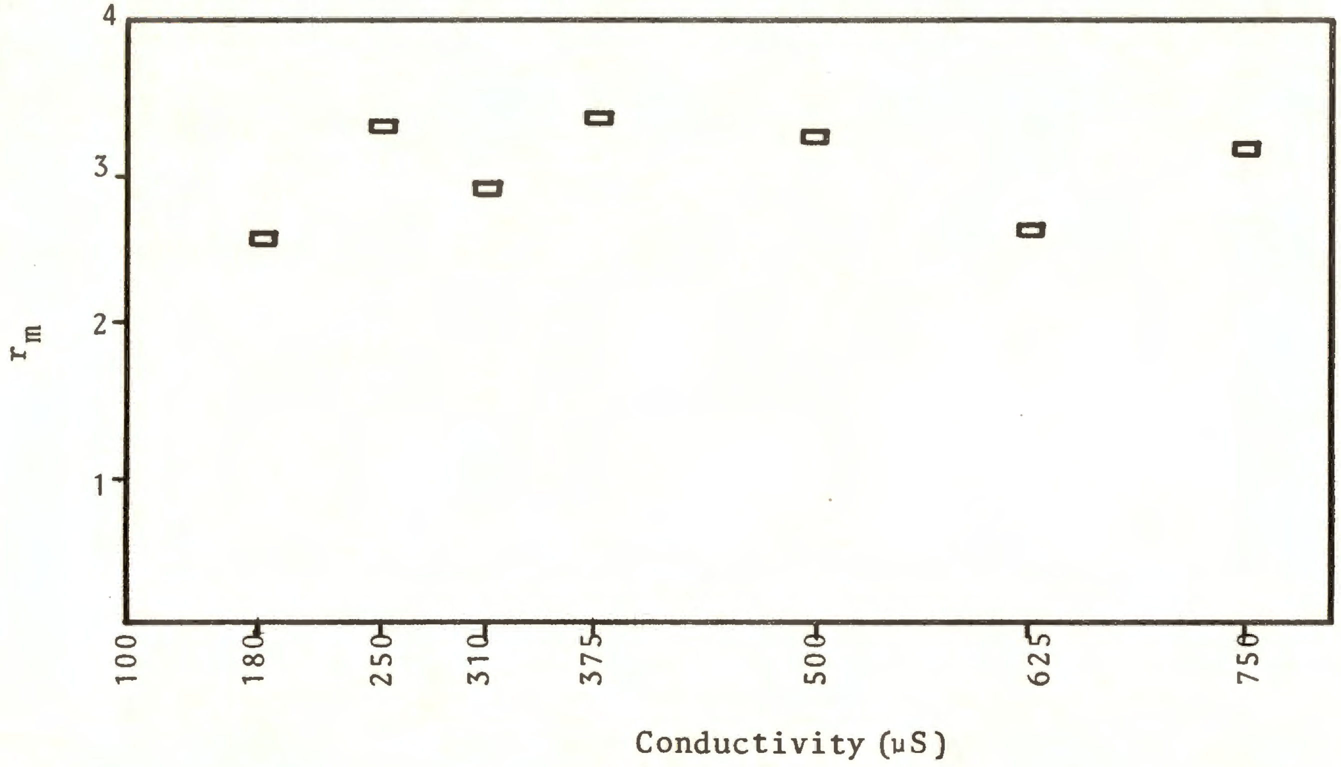


Figure 86. A graphical representation of the intrinsic rate of natural increase (r_m) of *B.pfeifferi* at the various constant conductivities

species is able to exist and multiply successfully at conductivities other than those within the 310 to 625 μS range and that the extremes of its tolerance in respect of conductivity lies below 180 μS and above 750 μS.

Williams (1970a & b) demonstrated that *B.(P.) globosus* has a wider tolerance to chemical conditions than *B. pfeifferi,* but the very small difference between the ranges of r_m values calculated for these two species in the present study suggest that their requirements in respect of water chemistry might, in fact, be very similar. It seems fairly certain that neither of these two species should be seriously affected by conductivities between 180 μS and 750 μS, that both should be most successful within the range 310 μS to 500 μS and that both should be severely affected below 180 μS and above 750 μS.

During a later phase of this study the conductivities were increased and decreased stepwise for the same cohort of each of the four species concerned. Both *B.(P.) globosus* and *B. pfeifferi* survived fairly successfully and for a considerable period at a conductivity of 50 μS but, as is evidenced by a drop in egg production and a rise in death rate, they were markedly affected as conductivities increased to 850 μS. Van Eeden, Brown & Oberholzer (1965), Shiff & Husting (1966), Shiff & Garnett (1967) an de Kock (1973) describe the ideal habitat for *B. pfeifferi* as one where warm stable conditions predominate and it seems unlikely that, under these conditions, conductivity would ever constitute any threat to its existence.

Harrison & Shiff (1966) and De Kock (1973) came to the conclusion that *B.(P.) globosus* is adapted for the fast colonization of warm temporary habitats. As habitats of this nature are subject to a high rate of evaporation with a consequent rise in salinity their conclusion would attribute this species with the ability to master this hazard. According to the results of the present study this seems to be true provided that the conductivity does

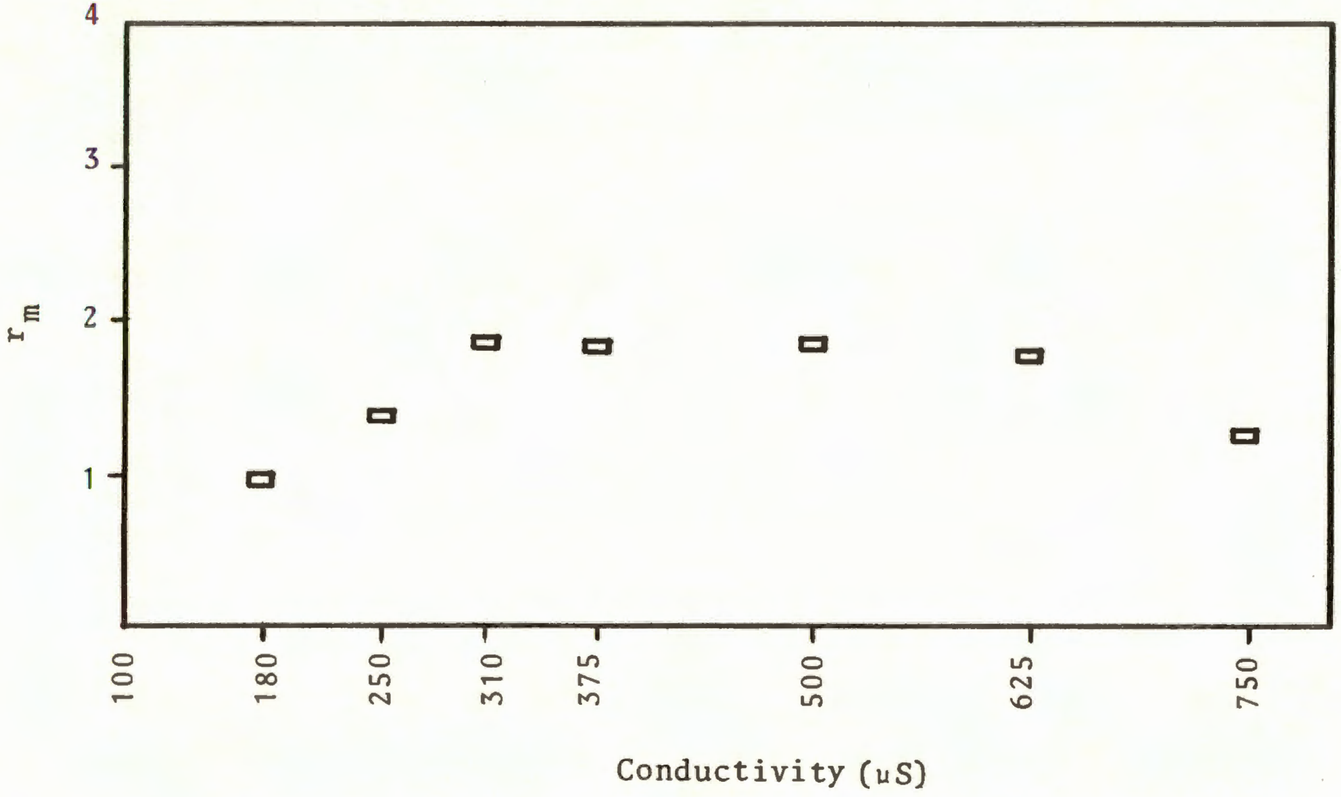


Figure 87. A graphical representation of the intrinsic rate of natural increase (r_m) of *B.(P.)globosus* at the various constant conductivities

not rise much above 850 µS and these high salinities do not last long because, if they do, they are inimical to the eggs and young snails and may therefore completely disrupt the propagation of the species. High salinities may, therefore, under particular circumstances, be a limiting factor to *B.(P.) globosus*.

The r_m values calculated for *L. natalensis* in the present study indicated a definite peak at 250 µS (figure 88) and the r_m range of 1,0355 reflected sensitivity to changes in conductivity. There were, moreover, definite indications that this species was markedly affected by salinity, particularly so in the higher ranges. Although 58,14% of the eggs hatched at a constant con= ductivity of 500 µS these hatchlings were unable to survive. Furthermore, during the experiment in which the conductivity was increased stepwise for the same cohort both fecundity and sur= vivorship were affected. As the conductivity was raised above 450 µS egg production dropped sharply and as it was raised still further mortalities occurred at a higher rate (figure 65). This was the only species of which a few specimens could be bred and maintained at 125 µS and together with *B. pfeifferi* this species recorded the highest hatching percentage at 180 µS. *Lymnaea natalensis* would not, therefore, be expected to colonize tempo= rary habitats which may be subject to drying up and rising con= ductivities. This probably explain De Kock's (1973) finding that its geographic distribution in South Africa is determined by the availability of suitable permanent habitats and not by prevailing temperatures. In the light of the present research the suitability of the permanent habitat seems to be largely determined by the salinity of its water which should not very much exceed 400 µS.

The low r_m values calculated for the cohorts of *B.(B.) tropicus* at 310, 375 and 500 µS obviously do not fit into the overall pattern of performance of this species (figure 89) and it might not be unreasonable to expect, judging from the performances of the cohorts at 250 and 625 µS, that its performance should have

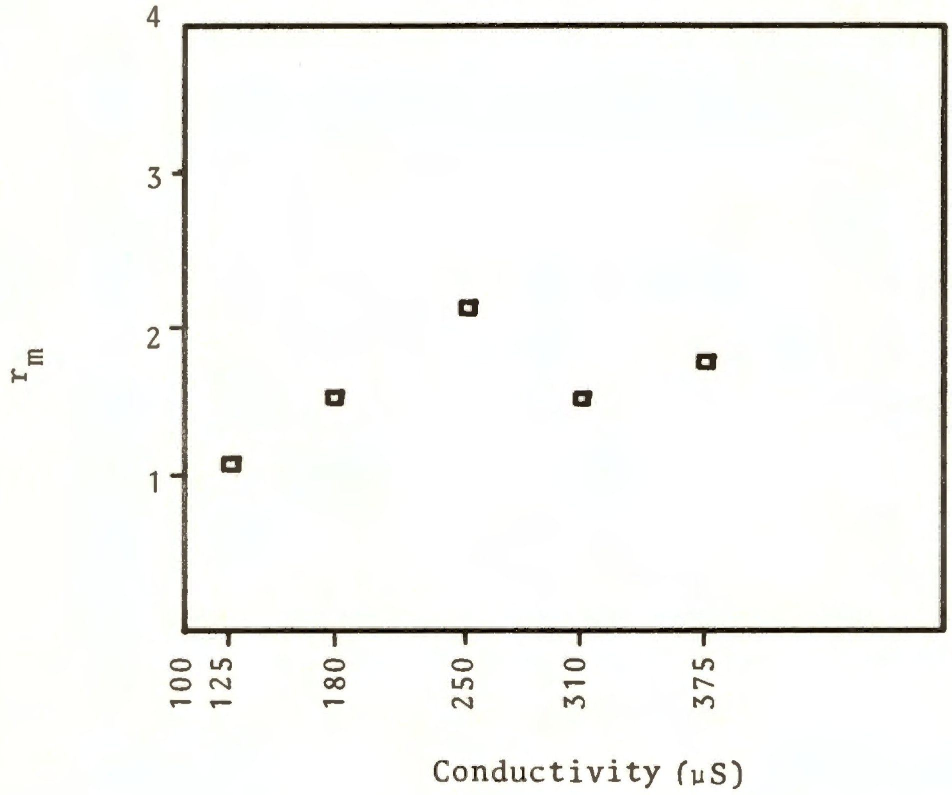


Figure 88. A graphical representation of the intrinsic rate of natural increase (r_m) of *L.natalensis* at the various constant conductivities

been much better at the first mentioned conductivities. This assumption is supported by the fact that De Kock (1973) recorded seven r_m values ranging from 3,3726 to 3,6644 for *B.(B.) tropicus* at a conductivity which fluctuated round about 400 μS. De Kock's r_m values as well as the results of this study recorded at 625 μS seem to point to the range 375 to 625 μS as being optimally suited for *B.(B.) tropicus*. It was evident that this species experienced a certain degree of stress at 180 μS which should therefore be regarded as sub-optimal for it. Whereas *L. natalensis* displayed a definite preferance for waters with low salinities, *B.(B.) tropicus* seemed to favour waters with higher conductivities.

According to De Kock (1973) the wide range of r_m values which he obtained for *B.(B.) tropicus* at constant temperatures ranging from 17°C to 32°C and the high r_m value recorded at 26°C all demonstrate the excellent adaptation of this species for colonizing temporary habitats in which the temperature fluctuates greatly and which dries up periodically. He finds support for this conclusion in the fact that in South Africa *B.(B.) tropicus* inhabits, amongst others, the arid parts of the country where other species are unable to exist as a result of the temporary nature of the habitats. Its tremendous reproductive capacity and short mean generation time under all conditions and its tolerance of temperature extremes enables it to recover from catastrophies within a short space of time and to build up sufficient numbers to ensure the continued survival of the species. Additional support for this conclusion is to be derived from the results of the present study, which demonstrated that *B.(B.) tropicus* has a greater tolerance for high salinities than any of the other species evaluated. The conductivity of 625 μS at which the highest r_m value for *B.(B.) tropicus* was recorded is, in fact, much higher than the optimum conductivities determined for any of the other species. Furthermore, a net reproductive rate of 1 587,80 was recorded for *B.(B.) tropicus* at 1 000 μS and the indications were that even higher conductivities would have been tolerated. Still in agreement with this line of

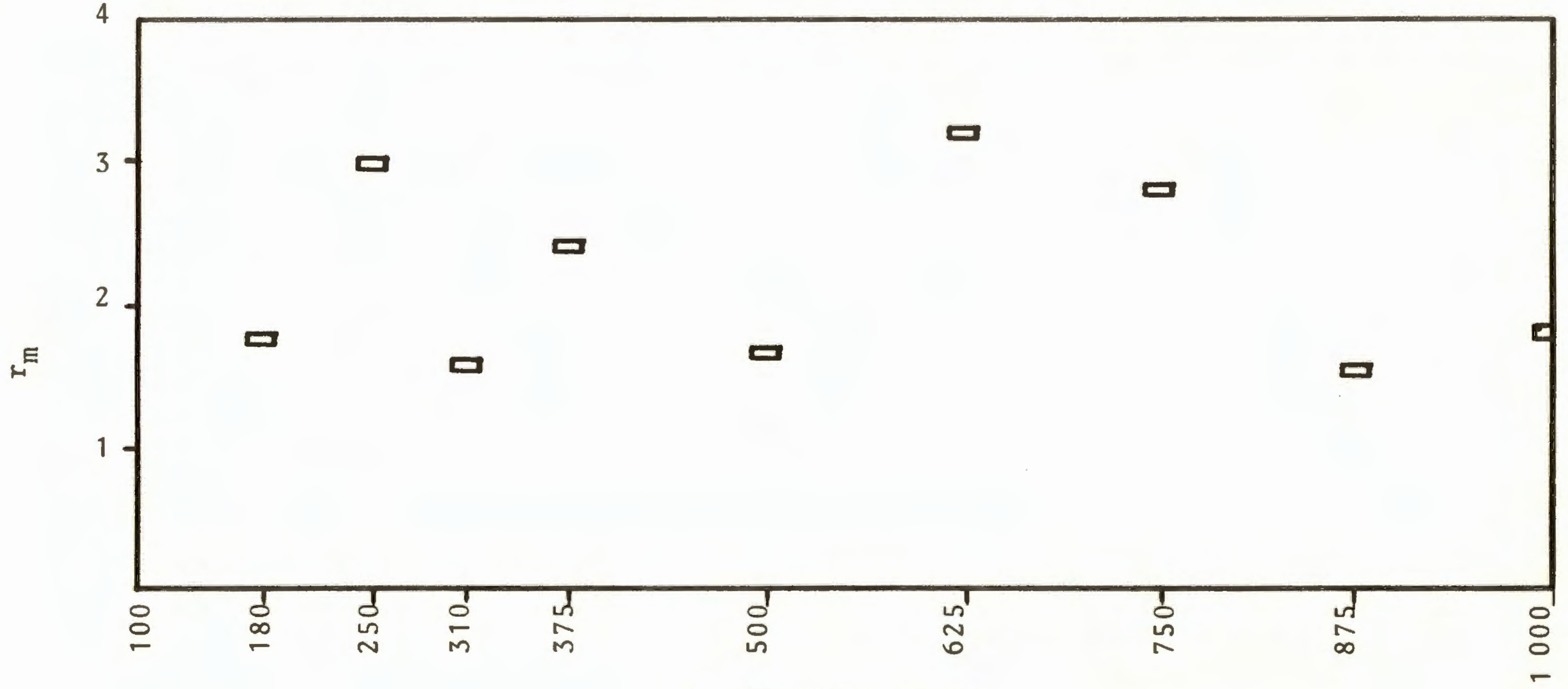


Figure 89. A graphical representation of the intrinsic rate of natural increase (r_m) of *B.(B.)tropicus* at the various constant conductivities

thought are the indications that this species was at a distinct disadvantage at the lower conductivities. Signs of this were particularly obvious at 180 μS where severe osmoregulatory problems were experienced by many of the specimens. In the experiment where the conductivity was stepwise lowered, egg production was unfavourably affected (table 42) and dropped off sharply as the conductivity was decreased below 150 μS. At 50 μS it had practically ceased and below this no eggs were deposited. All these data make it abundantly clear that *B.(B.) tropicus* can tolerate extremely high salinities much better than it can relatively low salinities and that its optimum salinity is higher than that of any of the other three species investigated.

The foregoing findings cast new light on the interesting geographical distribution in the Republic of South Africa of *B.(B.) tropicus, L. natalensis, B.(Physopsis)* species and *B. pfeifferi*, first spotted and discussed by Van Eeden & Combrinck (1966). The position is that the last mentioned three species not only enjoy very much the same distribution, except that the range of *L. natalensis* is more extensive than that of *B.(Physopsis)* spp. of which, in turn, the range is more extensive than that of *B. pfeifferi*, but they almost as often as not share the same habitat. In contrast to this *B.(B.) tropicus* hardly ever shares a habitat with any one of these three species and is not at all common in the areas inhabited by them. Thus Schutte & Frank (1964) failed to find *B.(B.) tropicus* in the Nelspruit/Barberton area and it enjoys only a sporadic distribution in north eastern Transvaal, northern Natal and Zululand (Van Eeden <u>et al</u>., 1965) as well as Mozambique (De Azevedo, 1961) where the other three species are very common. Wherever, on the other hand, *B.(B.) tropicus* is common *L. natalensis* may occur at low densities in places, *B.(Physopsis)* spp. is extremely rare and *B.(B.) pfeifferi* is completely absent. Although it could be argued that *B.(B.) tropicus* outcompetes the other three species in the latter situation, which is now known not to be true, none of the facts until recently known regarding its ecological requirements could explain its absence from the first mentioned areas. It has been known all along that the waters in these areas have a rather low dissolved solid content which, although not harmful to either *L. natalensis*, *B.(Physopsis)* spp. or *B. pfeifferi*, now turned out to be so unacceptable to *B.(B.) tropicus* that it percludes colonization of these areas by the latter species.

It is clear from the results so far discussed that the chemical quality of the water constitutes a very important factor in de=termining the distribution of at least some freshwater snail species. In contrast to the views of Helmy (1953), Marill (1953), Deschiens (1954, 1957), Alves (1958) De Meillon et al. (1958) and Schutte & Frank (1964) who all concluded that the distribution of snails is independent of water chemistry, a great deal of evidence suggests the opposite. It is now gene=rally acknowledged that the mineral quality of the water has a definite and important effect on the snails but only when limi=ting concentrations are approached. For most factors, however, there is a wide range of tolerance. From the point of view of snail control, unfortunately, the different species are differentially tolerant to most of the factors which affect them so that what applies to one species need not be true for another one.

Quite often snails are absent from waters where the apparent cli=matic and ecological conditions seem eminently suited for their existence. An example of this is the absence of *B.(B.) trunca=tus* from the waters of Abadan Island as well as certain waters in Basrah in Southern Persia where, despite conditions which Watson (1953) describes as apparently ideal, this species has been unable to establish itself. Watson (1953) suspects one of the possible factors prohibiting the colonization of these waters to be the occurrence of periods of exceptionally high salinities which rise high enough to be rapidly lethal to all the populations of *B.(B.) truncatus* in the area. Watson (1958) also blames the absence of this species from many waters in the Middle

East and North Africa on the rise in salinity which accompanies the intensive evaporation in these areas. An important fact underlined by this author, which is also substantiated by some of the results of the present study, is that high salinities which are more lethal to the eggs and young snails, can be tolerated by adult specimens through a process of gradual acclimatization. This might enable them to survive adverse periods and to resume reproduction when conditions become favourable for the hatching of eggs and survival of the young. On the other hand a factor which is harmless to the adults may preclude colonization of an area by reason of the effect it has on breeding. Watson (1958) also considers the existence of several ecological races with differing reactions to environmental factors to be a definite possibility which would explain certain discrepancies which may become apparent in a study of the tolerance of a species to certain factors. The possible existence of different snail races is also mentioned by Gaud (1958) and evidence to support this theory is supplied by Forbes & Crampton (1942) and Harrison (1966).

The absence of *B.(B.) contortus* from certain waters in Libia, particularly in the small lakes around Benghazi and in the Tanorga River, is the result of very high salinities in these habitats according to Zavattari (1938) who found the distribution of this species to be very closely linked with the chemical composition of the water.

The inimical effect that rising salinities, caused by evaporation, exercises over snail populations has also been observed by Mandahl-Barth et al. (1972) who found that snail populations rapidly deteriorated during the dry season in Katanga when salinities increased tremendously as a result of evaporation. During the rain season snails again became abundant when these waters were diluted by rain. This phenomenon could, of course, also be partly attributed to drastic rises in temperature. It is a well known fact that not only seasonal temperatures but also the magnitude of diurnal fluctuations may approach extremes in habitats subjected to partial or complete drying out.

It is, however, not only high salinities that have a detrimental effect on the snails. Several observations indicate that very often a shortage of dissolved solids prevents the colonization of certain areas or water bodies by particular aquatic snail species.

Mozley (1944) found that bilharziasis intermediate host species very seldom occur in waters which contain less than 10 ppm dissolved salts (estimated by electrical conductivity) in Rhodesia and he also records his inability to find them in waters with a dissolved solid content in excess of 430 ppm.

In Puerto Rico the physico-chemical composition of the water plays an important role in limiting the distribution of *B. glabrata* (Harry & Cumbie, 1956a & b, Harry et al., 1957 and Harry & Aldrich, 1958). Here these authors found this species to be absent from most waters containing small amounts of dissolved solids. According to their findings the concentration of dissolved solids in the fresh waters in Puerto Rico ranges from about 50 to 3 000 ppm. Although they consider the best snail habitats to be those which contain 150 to 500 ppm they also recovered snails from waters with concentrations up to 3 000 ppm. Only rarely, however, did they find snails in waters with concentrations consistently lower than 150 ppm.

It is, therefore, clear that the mineral content of the water has a very definite effect on the snails when limiting values are approached, but it has become equally clear that the total dissolved solids is less critical than the proportions in which certain constituent salts are present. Threshold and ceiling values have been determined for individual dissolved solids and considerable differences exist between the different species as regards their tolerances. They are, therefore, affected differntly by the same concentrations. It seems obvious that, in nature, catastrophic changes in this respect seldom occur but should this happen it would invariably have fatal consequences for the snails.

Experimental work in this connection has been carried out by Van Someren (1946), Vermeil et al. (1952), De Azevedo et al. (1954), Deschiens (1954), Litalien & Deschiens (1954), Dechange & Deschiens (1955), Alves (1956), Abdel-Malek (1958), Harrison et al. (1966), Harrison (1968), Harrison et al. (1970), Williams (1970a & b), Liang (1971) and Lo (1972). These authors tried to determine the requirements and tolerances of snails to certain cations and anions as well as dissolved minerals in general. Williams (1970 a & b) attempted to discover the relationship between the distribution and relative densities of five common freshwater snail species and the calcium bicarbonate concentration of the aquatic environment. The waters were classified according to their calcium bicarbonate content. Waters were regarded as soft when they contained <5mg/l Ca^{++} and <20 mg/l HCO_3^-; water with 5 to 40 mg/l Ca^{++} and 20 to 200 mg/l HCO_3^- was classified as medium hard and water with <40 mg/l Ca^{++} and 200 mg/l HCO_3^- as hard. Following this classification the water used in the present investigation should be classified as medium. According to Williams the distribution of certain species could be correlated with certain concentration ranges of the calcium and bicarbonate ions. Thus *Bulinus (B.) tropicus* was restricted to medium water, *B. pfeifferi* was found only in medium and hard waters and *B.(P.) globosus* and *L. natalensis* were found in all water types, although their densities were lower in soft water. In general it was concluded that soft water was unfavourable for these snails.

In a study on the effects of calcium bicarbonate concentrations on the biology of *B. pfeifferi*, Harrison et al. (1970) support Williams' (1970a & b) contention that different levels of calcium and bicarbonate concentration can have a marked effect on the biology of this species. In their study which was an attempt to determine differences in reaction of different populations to calcium bicarbonate concentrations the same general pattern of performance was obtained for all the populations studied although the best performances were recorded for the medium water. Harrison (1968) also demonstrated that the oxygen uptake of *B. pfeifferi* was best in medium water.

Although, for both *B.(P.) globosus* and *B. pfeifferi*, Williams (1970b) recorded the highest r_m values in medium water the range of r_m values for the latter was wider (0,42) than that for the former (0,17). Williams regards this difference as important since the species with the wider range must be more sensitive to differences in bicarbonate concentrations than the others. This agrees with the findings of Harrison & Shiff (1966) who conclude that *B. pfeifferi* not only appears to be particularly intolerant of low bicarbonate concentrations but also reacts to abnormally high ones.

An analysis of the data contained in table 2 reveals that although most of the waters used during the present experiment conform to the requirements of the medium water as described by Williams (1970a) (except the waters with conductivities of 50 μS and 1 000 μS) the average calcium content was not very high. Only the waters with conductivities of 500 and 625 μS and a calcium content of 18 and 19 ppm came close to satisfying the requirements of Williams' medium water and Frank's optimum calcium carbonate concentrations for *B. pfeifferi*. The waters with conductivities of 125 μS, 180 μS and 875 μS, on the other hand, were very near to the minimum requirements in this respect.

In the description earlier on, of how waters with high conductivities were obtained for the present investigation it was stated that the evaporation process was speeded up by heating the water. As the conductivity of this water increased it became saturated with calcium carbonate and calcium sulphate and these salts precipitated out as a white deposit on the bottom of the evaporation tanks. This process of precipitation, which was possibly accelerated by the heating of the water, significantly lowered the calcium content of the water at the higher conductivities (table 2) but left the magnesium and sodium content untouched. The result of this was that at 1 000 µS the magnesium/calcium ratio was more than 100:3 and at 875 µS this ratio was more than 100:7. Viewed against the background of the results obtained by Alves (1958), Abdel-Malek (1958), Frank (1964) and Harrison et al. (1966) these facts cast additional light on the performance of the cohorts at the high conductivities in the present investigation.

Although Alves (1958) concluded that *Bulinus (Physopsis)* and *Biomphalaria* habitats were rich in both calcium and magnesium he also found that if the magnesium content was greatly in excess of calcium the habitat usually was free of snails. This observation was confirmed by Harrison et al. (1966) who showed that aquatic snails were absent from streams with water high in dissolved magnesium but comparatively low in dissolved calcium. They, furthermore, established that egg laying rates of *B. pfeifferi* were significantly lower in the water with high magnesium/calcium ratios and that no eggs were produced at a ratio of 19:7. In contrast to this Schutte & Frank (1964) found a magnesium/calcium ratio of 467:54 to be not unfavourable to snails. There is, however, general agreement with the statement of Abdel-Malek (1958) that small quantities of magnesium in the habitat water are necessary for the snails but that an excess of magnesium is unfavourable. In the present study only *B.(B.) tropicus* could be bred with some degree of success at 875 and 1 000 µS and the absolute failure of the other three species to breed at these two conductivities could very well have been due to an unfavourable magnesium/calcium ratio. This was 100:7 at 875 µS and 100:3 at 1 000 µS respectively. In view of the very high magnesium and low calcium content of the water at 875 and 1 000 µS (table 2) the ability of *B.(B.) tropicus* to exist successfully in this water is all the more remarkable.

In addition to the magnesium/calcium ratio considerable importance has been attached to the sodium/calcium ratio. Abdel-Malek (1958) is of opinion that water with a high concentration of sodium as compared to other cations, especially calcium, is unfavourable to the snails. Frank (1963) concluded that water with a calcium carbonate concentration of approximately 18 ppm and a sodium/calcium ratio of one was best suited for growth and fecundity of *B. pfeifferi*. Schutte & Frank (1964) noted that both *Bulinus (Physopsis)* and *Biomphalaria* were always present in water with a sodium/calcium ratio of between 0:5 and 2:0, whilst the former was always present and the latter uncommon in waters with a ratio above 2:4.

In the present study the ratio of sodium/calcium at 1 000 µS was 14,6:1 and 4,43:1 at 875 µS. At 750 µS this ratio was 2,55:1 and at 625 µS 1,11:1. From these values it can be seen that the ratios at 1 000 µS and 875 µS must definitely have been unfavourable to the snails if the findings of the authors cited above be accepted. The fact that, as in the case of the extremely unfavourable magnesium/calcium ratio's, only *B.(B.) tropicus* could be bred at both these conductivities with equally unfavourable sodium/calcium ratio's, once again reflects the exceptional tolerance of this species for extreme saline conditions. It seems justifiable to blame the failure of both *B.(P.) globosus* and *B.pfeifferi* to breed at 875 µS and 1 000 µS on the unfavourable sodium/calcium and/or magnesium/calcium ratio's.

The specific distribution pattern of *L. natalensis* near Salisbury as recorded by Williams (1970a) shows that it has a distinct preference for soft and medium waters. This observation is substantiated by the fact that it was the only one of the four species used in the present investigation that could be bred with any success at 125 µS. Furthermore, it was the species least tolerant to stepwise increasing salinities as its failure to breed at 500 µS and higher indicates. The results of this study, therefore, indicated that, for the particular water used in these experiments, the highest tolerance to conductivity of *L. natalensis* lies between 375 and 500 µS. Van Someren (1946) concludes that *L. caillaudi* prefers water with a calcium carbonate content of 10-19 ppm but he suspects that the lower limit of tolerance of this species probably lies somewhere round about 8 ppm or below that.

One of possibly many different reasons for the failure of snails to survive at very low and very high salinities could perhaps be sought in their inability to overcome the problem of osmoregulation at such salinities. According to Deschiens (1956) and the WHO (1956) it is particularly the eggs and immature forms that are vulnerable in this respect. These views are supported by the experimental evidence obtained during the present study. Although the effects of the lower and higher conductivities have been discussed elsewhere, they will be briefly repeated here. At 125 µS a certain percentage of the eggs of *B. pfeifferi*, *B.(P.) globosus* and *B.(B.) tropicus* were able to hatch but in all three cases these hatchlings died within a short time. At 500 µS a large percentage of the eggs of *L. natalensis* hatched but again the juveniles died shortly after hatching. In another experiment discussed elsewhere, however, the conductivity of the water was lowered to 500 µS and in spite of this the species of which the eggs and young ones were unable to hatch or survive at 125 µS showed no signs of distress. On the contrary, the lowering of the conductivity seemed to induce a sudden burst of egg production by *B. pfeifferi*.

In yet another experiment where the conductivity was increased to values where hatching had failed previously the adult snails were able to survive without any apparent distress and fecundity was not affected drastically except in the cases of *B.(P.) globosus* and *L. natalensis*. In both these species a sharp drop in egg production and an increase in mortality occurred as the conductivity started increasing above 650 µS.

At a conductivity of 180 µS it was apparent that the osmoregulatory mechanisms of *B.(B.) tropicus* and *B. pfeifferi* were unable to prevent the absorbtion of excess amounts of water. Although this phenomenon was not manifested in every snail, more than half of the specimens in these two cohorts suffered from it. In many cases the snail became swollen to at least twice its original size. In this condition the snails were unable to retract into their shells and were completely immobilized. The eventual result was a prolonged death.

Pimentel & White (1959) observed very similar reactions in *B. glabrata,* when they were placed in water with a conductivity of 5 µS. In two groups of snails obtained from different localities the mortality rate was 100% and 80% respectively. The reaction of the snails to the water was hemorrhaging and swelling. In this case the snails became so bloated with water that in many cases their bodies burst open. It is interesting to note that the group of snails in which the mortality was only 80% were originally recovered from a habitat that had a much lower conductivity than the habitat from which the other group with 100% mortality were recovered. These authors observed a burst of egg laying when the snails were placed in their low conductivity environment.

In contrast to the foregoing Harry et al. (1957) maintained adult specimens of *B. glabrata* for two weeks in redistilled water without any apparent harmful effects. The eggs apparently developed at the normal rate but the unhatched snails seemed to have difficulty in escaping from the gelatinous egg clutch and very few managed to hatch successfully. These authors conclude that while it is evident that adult snails can withstand waters with little dissolved solids for at least short periods it is equally evident that such waters may be unfavourable for eggs and juveniles.

Finally it does appear as if the statement of Hubendick (1958) is applicable to the results obtained during the present study. This author states that it is generally thought that among fresh=

water snails the optimum conditions are mostly rather similar, but the tolerable ranges often differ slightly, though seldom to a great extent. This means that the habitat requirements of the various species may often overlap although they are not completely identical because their ecological requirements are qualitatively similar but quantitatively different. He concludes that freshwater snails are decidedly euryok, like so many other freshwater creatures.

This theory is true for the snails studied in the present investigation. To a great extent the trend of the reaction of all the species was very similar but they revealed different degrees of sensitivity to the various conductivities.

From the results obtained it may be concluded that whereas the geographical distribution of *B. pfeifferi* and, to a lesser extent that of *B.(P.) globosus*, is not determined by the prevailing conductivities in the natural habitats, this factor must definitely be counted as one of those which determine the distribution of both *L. natalensis* and *B.(B.) tropicus*. It was, however, observed to have opposite effects on these two species. As a result of its ability to survive at very high salinities *B.(B.) tropicus* is ideally suited to exploit, among others, temporary habitats which are unsuitable for most other species but it is unable to colonize waters with permanent low conductivities. In contrast to this *L. natalensis* is restricted to permanent stable water=bodies where conductivities do not rise higher than 500 µS for very long periods.

5. SUMMARY

1. Life tables were compiled using cohorts of *B.(P.) globosus, B. pfeifferi, L. natalensis* and *B.(B.) tropicus* at constant con=ductivities of 125, 180, 250, 310, 375, 500, 625, 750, 875 and 1 000 μS.

2. Life tables were compiled for *B. salinarum* and *B.(P.) afri=canus* at 900 μS.

3. Adaptation and acclimatization by the same and successive generations to unfavourable conditions were studied.

4. The population statistics R_o, T_c, r_m, r_c and λ were calcu=lated from the data contained in life tables.

5. The mean fortnightly growth rate per snail was determined for all the species mentioned under the first statement.

6. Chemical conditions of the culture waters were carefully monitored and controlled.

7. A technique was developed according to which only a fraction of the weekly egg production of *L. natalensis* needs to be counted.

8. The breeding and maintenance of freshwater snails under experimental conditions is discussed.

9. Intra and inter species comparisons of performance at the various constant conductivities were made.

10. The highest values for the different population statistics were not necessarily recorded at the same conductivity or by the same cohort of snails.

11. Evidence was found that salinity at the values occurring in the permanent natural freshwaters has no profound

effect on the biology of *B. pfeifferi* and *B.(P.) globosus.*

12. The distribution of *L. natalensis* seems to be restricted by high salinities.

13. The distribution of *B.(B.) tropicus* is to a great extent limited by low salinities.

14. In all four species salinity has a greater effect on the eggs and juvenile stages than on the adult snails and it is mainly as a result of this that the total effect of this factor on snails is manifested.

15. The four species investigated exhibited different optimum requirements as regards conductivity.

16. Both *B. salinarum* and *B.(P.) africanus* are able to survive at high conductivities.

17. Definite indications of adaptation and acclimatization to changing conductivities were found.

18. The influence of salinity on the geographic distribution and habitat selection of freshwater snails investigated is discussed.

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8. APPENDIX

Table A1 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 125 µS.

Fortnights	$\%O_2$			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	100,0	100	100	0,58	0,6	0,8
2	99,8	99	100	1,30	1,2	1,4
3	98,7	97	100	1,20	0,9	1,5
4	98,7	97	100	3,90	3,1	4,6
5	94,9	90	97	5,00	5,0	5,0
6	96,8	94	100	4,60	3,7	5,6
7	93,0	88	94	5,25	5,2	5,3
8	97,0	95	99	5,00	3,1	6,9

Table A2 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at180µS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	99,80	99	100	0,73	0,2	1,1
2	97,70	94	99	1,60	1,1	2,1
3	97,80	94	100	3,90	3,5	4,3
4	96,60	95	97	4,00	2,8	5,2
5	97,00	93	99	5,20	5,2	5,3
6	97,20	95	100	6,00	5,2	6,9
7	98,30	97	100	5,00	3,0	7,1
8	99,30	99	100	3,80	3,6	4,0
9	97,30	95	100	5,00	3,6	6,5
10	98,80	97	100	4,40	4,2	4,6
11	100,00	100	100	5,30	5,3	5,4
12	99,75	99	100	4,80	3,7	5,9

Table A3 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 250µS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	100,0	100	100	0,55	0,5	0,6
2	99,8	99	100	1,80	0,3	3,2
3	97,4	96	100	4,60	3,5	5,7
4	94,4	88	97	5,80	5,7	5,9
5	96,3	93	100	6,30	5,9	6,7
6	94,8	94	95	6,70	6,5	7,1
7	93,7	90	97	5,50	4,8	6,2
8	96,0	93	100	6,10	6,0	6,3
9	98,3	97	100	5,80	4,5	7,1
10	99,8	99	100	4,00	3,2	4,9
11	97,3	95	100	3,90	3,8	3,9
12	98,5	97	100	4,00	3,8	4,2
13	100,0	100	100	4,30	3,8	4,7

Table A4 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 310µS.

Fortnights	$\%O_2$			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	98,4	94	100	1,4	1,0	2,0
2	99,8	99	100	2,8	2,2	3,8
3	98,6	95	100	4,0	3,1	5,6
4	97,5	97	99	4,8	4,4	5,1
5	97,8	97	100	6,1	6,0	6,2
6	99,0	97	100	6,3	6,0	6,6
7	99,8	99	100	4,5	3,9	5,1
8	99,3	99	100	4,6	4,0	5,1
9	99,8	99	100	4,4	4,3	4,5

Table A5 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 375µS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	99,5	99	100	0,45	0,3	0,6
2	98,3	95	100	1,40	0,6	2,2
3	97,3	96	100	3,10	2,9	3,3
4	96,1	94	100	6,60	6,3	6,9
5	97,4	94	100	7,00	6,9	7,1
6	96,0	95	100	3,80	2,7	4,9

Table A6 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 500µS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	99,4	94	100	1,30	1,0	2,1
2	96,3	95	100	5,00	4,7	5,3
3	96,8	94	100	3,40	2,8	4,0
4	98,0	95	100	5,45	5,3	5,6
5	94,8	94	95	4,00	3,3	4,8
6	96,3	94	97	5,00	4,5	5,5
7	96,6	94	99	5,90	5,8	6,0
8	97,3	95	100	5,60	5,4	5,8
9	96,8	95	100	5,80	5,8	5,8
10	96,5	95	97	5,60	5,6	5,6
11	99,3	99	100	5,75	5,7	5,8
12	96,5	88	100	6,00	5,9	6,1

Table A7 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 625μS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	100,0	100	100	2,05	1,6	2,7
2	100,0	100	100	3,80	2,8	4,8
3	100,0	100	100	6,30	6,2	6,5
4	99,5	99	100	6,60	6,5	6,6
5	99,0	99	99	6,50	6,5	6,5
6	100,0	100	100	3,20	1,6	4,8
7	100,0	100	100	3,50	3,2	3,8
8	100,0	100	100	4,05	3,9	4,2
9	100,0	100	100	4,15	5,1	4,2
10	100,0	100	100	3,40	3,2	3,6
11	100,0	100	100	2,15	1,2	3,1

Table A8 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 750μS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	100,0	100	100	2,00	1,6	2,7
2	100,0	100	100	4,55	3,6	5,5
3	100,0	100	100	5,55	5,5	5,6
b 4	95,0	90	100	6,25	5,9	6,6
5	99,0	99	99	6,50	6,5	6,5
6	98,5	97	100	4,10	2,8	5,4
7	98,5	97	100	4,15	2,6	5,7
8	100,0	100	100	5,20	5,2	5,2
9	100,0	100	100	4,70	4,6	4,8
10	100,0	100	100	3,90	3,6	4,2
11	100,0	100	100	3,35	3,2	3,5
12	100,0	100	100	1,15	1,1	1,2
13	100,0	100	100	0,80	0,8	0,8

Table A9 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 875µS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	96,3	87	100	1,70	1,2	2,5
2	98,0	95	100	3,10	3,0	3,2
3	97,0	95	99	3,10	2,1	4,1
4	99,0	99	99	5,60	5,6	5,6
5	99,3	97	100	6,40	6,2	6,5
6	98,8	97	100	6,05	5,7	6,4
7	99,3	97	100	6,60	6,5	6,6
8	100,0	100	100	6,60	6,6	6,6
9	94,8	93	97	5,05	4,7	5,4
10	97,3	97	100	4,80	4,0	6,1

Table A10 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at 1 000µS.

Fortnights	%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	98	90	100	0,85	0,5	1,2
2	98,8	97	100	1,60	0,7	2,5
3	96,0	90	100	2,80	2,0	3,5
4	94,0	93	95	4,40	4,2	4,5
5	94,3	90	99	5,20	4,2	6,2
6	97,3	95	100	6,00	5,5	6,5
7	99,3	99	100	6,70	6,6	6,7
8	98,8	95	100	6,00	5,6	6,4
9	98,4	97	100	6,40	6,4	6,4
10	99,3	97	100	6,70	6,7	6,7

Table A11 Mean minimum and maximum fortnightly values of percentage saturation with oxygen and B.O.D. (kg/m^3) at stepwise increasing and decreasing salinities.

	250µS-increased						250µS-decreased					
Fort=nights	%O_2			B.O.D.			%O_2			B.O.D.		
	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.	$\bar{x}$	min.	max.
1	100,0	100	100	2,3	1,2	3,1	100,0	100	100	2,0	1,3	2,6
2	100,0	100	100	4,9	3,5	6,2	100,0	100	100	3,8	2,9	4,6
3	99,5	99	100	6,3	6,0	6,6	100,0	100	100	5,7	5,6	5,8
4	100,0	100	100	6,7	6,6	6,7	98,5	97	100	6,4	6,3	6,4
5	98,5	97	100	6,6	6,5	6,7	99,0	99	99	6,5	6,5	6,5
6	99,5	99	100	2,9	2,8	3,0	99,5	99	100	4,8	3,0	6,6
7	100,0	100	100	5,2	5,2	5,2	99,5	99	100	2,9	2,5	3,2
8	100,0	100	100	4,7	4,2	5,2	98,0	97	99	3,7	3,3	4,0
9	100,0	100	100	4,9	4,6	5,2	100,0	100	100	4,1	4,0	4,2
10	100,0	100	100	2,5	2,4	2,6	100,0	100	100	3,5	3,4	3,6
11	-	-	-	-	-	-	100,0	100	100	3,0	2,6	3,3
12	-	-	-	-	-	-	100,0	100	100	2,0	1,8	2,2

Table A12 Mean fortnightly mass* of *B.(P.)globosus*.

Fortnights	Conductivities						
	180µS	250µS	310µS	375µS	500µS	625µS	750µS
1	0,0005	0,0022	0,0072	0,0056	0,0067	0,0040	0,0047
2	0,0043	0,0304	0,1089	0,0889	0,0787	0,0411	0,0507
3	0,0192	0,0829	0,2520	0,2157	0,1947	0,1494	0,1364
4	0,0666	0,1510	0,3538	0,2778	0,2867	0,2453	0,2199
5	0,1060	0,2253	0,4558	0,2989	0,3222	0,3018	0,2640
6	0,1451	0,2583	0,5196	-	0,3687	0,3499	0,3635
7	0,1899	0,2914	0,5913	-	0,4207	0,3771	0,3872
8	0,2433	0,3166	0,6337	-	0,4577	0,3798	0,4003
9	0,3204	-	0,6973	-	0,4793	0,3881	0,4393
10	0,4091	-	0,7253	-	0,5287	-	0,4762
11	0,5006	-	0,7254	-	0,5082	-	0,4366
12	-	-	0,7923	-	-	-	0,4367

*In grams

Table A13 Mean fortnightly number of egg clutches per snail produced by *B.(P.)globosus* at the various conductivities.

Fortnights	Conductivities						
	180µS	250µS	310µS	375µS	500µS	625µS	750µS
2	0	0	0	0	0	0	0
3	0	0	18,6	16,3	6,84	4,21	0,32
4	1,57	5,56	25,74	16,58	20,33	16,39	4,26
5	4,46	14,17	32,59	9,11	22,44	17,89	8,16
6	3,36	16,19	24,44	-	19,63	11,72	12,18
7	9,91	15,86	27,54	-	16,5	8,5	14,76
8	13,27	12,25	17,92	-	9,88	4,62	13,36
9	15,29	-	15,0	-	13,92	4,0	9,18
10	19,4	-	11,5	-	10,08	-	10,5
11	25,5	-	8,78	-	15,0	-	9,14
12	-	-	14,0	-	-	-	3,4

Table A14 Mean number of eggs per egg clutch of *B.(P.)globosus* per fortnight

Fortnights	Conductivities						
	180µS	250µS	310µS	375µS	500µS	625µS	750µS
2	0	0	0	0	0	0	0
3	0	0	4,09	4,96	9,61	9,88	3,33
4	5,09	12,13	7,36	8,04	13,41	15,87	7,68
5	10,19	16,58	10,97	12,06	18,75	20,93	12,97
6	16,68	19,76	11,45	-	19,18	18,90	18,21
7	15,66	22,76	12,29	-	19,57	20,32	20,46
8	16,84	15,18	13,30	-	17,82	18,27	20,91
9	17,34	13,17	12,32	-	16,27	16,47	17,51
10	19,63	-	10,03	-	19,42	17,88	19,26
11	22,08	-	4,65	-	17,67	-	18,36
12	-	-	3,35	-	-	-	16,53

Table A15 Mean fortnightly number of egg clutches per snail produced by *B. pfeifferi* at the various conductivities.

Fortnights	Conductivities						
	180µS	250µS	310µS	375µS	500µS	625µS	750µS
1	0,0015	0,0181	0,0081	0,0169	0,0176	0,0083	0,0147
2	0,0481	0,1189	0,0816	0,0953	0,0481	0,0584	0,0837
3	0,1375	0,1683	0,1260	0,1315	0,1447	0,0972	0,1300
4	0,1908	0,1840	0,1519	0,1430	0,1799	0,1260	0,1702
5	0,2125	0,2201	0,1729	-	0,1961	0,1711	0,1740
6	0,2367	0,2367	0,1805	-	0,2101	0,1870	0,1954
7	0,2665	0,2441	-	-	0,2251	0,2118	0,2204
8	0,2838	0,2787	-	-	0,2490	0,2206	0,2166
9	0,2865	-	-	-	0,2630	0,2551	0,2333
10	0,3011	-	-	-	0,2582	-	0,2499
11	0,3163	-	-	-	0,3022	-	0,2500
12	0,3169	-	-	-	0,3020	-	-

Table A16 Mean fortnightly number of egg clutches per snail produced by *B.pfeifferi* at the various conductivities.

Fortnights	Conductivities						
	180µS	250µS	310µS	375µS	500µS	625µS	750µS
2	2,25	11,00	6,80	11,06	10,90	3,40	8,25
3	19,68	21,35	16,80	19,46	19,90	11,65	19,80
4	20,47	19,00	14,20	-	16,45	12,16	15,26
5	17,26	22,44	13,69	-	15,10	15,79	12,58
6	16,11	18,06	16,54	-	16,70	16,84	18,63
7	20,05	18,00	-	-	15,17	15,29	15,61
8	16,56	-	-	-	15,35	12,67	16,11
9	18,24	-	-	-	12,71	-	20,33
10	18,00	-	-	-	14,94	-	18,00
11	19,19	-	-	-	15,78	-	-

Table A17 Mean fortnightly number of egg clutches per snail produced by *B.pfeifferi* at the various conductivities.

Fortnights	Conductivities						
	180μS	250μS	310μS	375μS	500μS	625μS	750μS
2	10,24	11,40	8,47	14,32	10,44	10,31	11,38
3	13,20	17,60	17,65	17,72	15,61	15,90	19,28
4	18,32	22,45	21,45	13,55	20,41	20,83	21,16
5	18,80	23,39	23,14	-	22,70	20,16	18,19
6	19,22	24,46	19,87	-	21,95	21,07	23,35
7	19,72	23,15	-	-	24,36	23,45	21,88
8	20,79	18,07	-	-	24,84	23,14	21,79
9	21,29	-	-	-	22,61	18,82	21,06
10	21,16	-	-	-	20,49	-	21,61
11	18,80	-	-	-	20,82	-	20,97
12	17,97	-	-	-	15,22	-	-

Table A18 Mean mass* of *L.natalensis* per fortnight.

Fortnights	Conductivities				
	125µS	180µS	250µS	310µS	375µS
1	-	0,0013	0,0054	0,0020	0,0044
2	0,0006	0,0088	0,0255	0,0616	0,1519
3	0,0353	0,1386	0,5832	0,2172	0,5295
4	0,3523	0,4614	0,8774	0,7327	0,5785
5	0,8646	0,6888	1,0112	0,5322	0,4795
6	1,2897	0,7073	1,0597	0,6949	-
7	0,8574	0,7683	0,9193	0,6943	-
8	1,1286	0,6410	-	-	-

*In grams

Table A19 Mean fortnightly number of egg clutches per snail produced by *L.natalensis* at the various conductivities.

Fortnights	Conductivities				
	125µS	180µS	250µS	310µS	375µS
2	0	0	0,05	0	0
3	0	2,43	5,56	1,80	5,59
4	3,20	7,38	13,06	9,90	15,80
5	6,80	15,08	17,17	15,36	23,00
6	8,75	15,33	14,33	21,00	-
7	21,00	9,83	12,00	29,00	-
8	17,00	-	-	-	-

Table A20 Mean fortnightly number of egg clutches per snail produced by *L.natalensis* at the various conductivities.

Fortnights	Conductivities				
	125µS	180µS	250µS	310µS	375µS
2	0	0	5,00	0	0
3	0	9,26	22,73	4,39	10,58
4	16,13	16,42	37,49	14,36	16,46
5	38,68	27,04	38,43	15,09	11,93
6	50,77	32,29	25,48	21,90	-
7	51,81	21,06	18,77	14,41	-
8	37,65	15,99	-	-	-

Table A21 Mean mass* of *B.(B.)tropicus* per fortnight.

Fortnights	Conductivities								
	180µS	250µS	310µS	375µS	500µS	625µS	750µS	875µS	1 000µS
1	0,0003	0,0163	0,0096	0,0241	0,0103	0,0094	0,0136	0,0033	0,0039
2	0,0113	0,1358	0,0508	0,1205	0,0705	0,1121	0,1151	0,0066	0,0070
3	0,0770	0,2836	0,0914	0,2394	0,1626	0,2487	0,2368	0,0538	0,1115
4	0,1456	0,3984	0,1505	0,3045	0,2340	0,3591	0,4571	0,1399	0,2264
5	0,1992	0,4303	0,1363	0,3147	0,2813	0,4550	0,4668	0,1802	0,3035
6	0,2715	0,5788	0,1752	-	0,3117	0,5100	0,5007	0,2129	0,3838
7	0,3522	0,6610	0,2107	-	0,3798	0,5118	0,5568	0,2673	0,4100
8	0,4137	0,7248	0,1913	-	0,3482	0,5629	0,6561	0,2682	0,4554
9	0,3815	0,7797	-	-	0,2940	0,6483	0,7226	0,5362	0,4595
10	0,2910	0,5510	-	-	-	0,7221	0,7963	0,5430	0,4853
11	-	-	-	-	-	-	0,9204	-	-
12	-	-	-	-	-	-	0,9683	-	-
13	-	-	-	-	-	-	0,9242	-	-

*In grams

Table A22 Mean fortnightly number of egg clutches per snail produced by *B.(B.)tropicus* at the various conductivities.

Fortnights	Conductivities								
	180µS	250µS	310µS	375µS	500µS	625µS	750µS	875µS	1 000µS
2	0,17	6,75	0	3,90	0,40	10,42	7,60	0	0
3	12,57	17,40	1,75	14,47	1,75	32,06	26,00	1,54	4,45
4	22,86	23,89	2,84	18,12	4,11	32,07	33,18	8,23	34,00
5	27,57	24,81	3,94	5,00	7,69	32,75	40,71	9,31	29,18
6	16,50	14,54	16,70	-	9,93	36,20	34,60	10,00	28,11
7	14,83	10,64	23,70	-	23,50	33,22	29,80	16,17	21,33
8	9,00	4,00	9,67	-	19,00	26,89	29,00	10,33	16,71
9	14,00	0,80	5,50	-	7,00	22,86	21,33	33,50	2,00
10	22,50	-	-	-	-	14,33	13,67	52,00	1,33
11	-	-	-	-	-	-	9,00	-	-
12	-	-	-	-	-	-	8,50	-	-

Table A23 Mean fortnightly number of egg clutches per snail produced by *B.(B.) tropicus* at the various conductivities.

Fortnights	Conductivities								
	180µS	250µS	310µS	375µS	500µS	625µS	750µS	875µS	1 000µS
2	6,50	11,10	0	6,53	10,88	10,65	6,50	0	0
3	11,57	13,05	18,63	8,20	16,00	14,47	13,15	16,05	13,41
4	15,86	18,41	23,35	13,66	10,38	20,71	18,13	19,06	18,75
5	14,92	18,25	27,30	8,72	15,28	19,98	19,43	28,81	25,31
6	15,90	15,14	17,29	-	18,42	20,06	24,83	21,28	26,28
7	11,63	13,39	20,18	-	20,08	18,70	26,11	21,88	29,00
8	7,26	8,47	23,59	-	29,05	17,79	22,36	18,69	27,72
9	11,79	3,25	17,58	-	27,81	14,64	23,36	21,04	22,08
10	8,56	-	-	-	-	12,86	24,00	19,44	12,25
11	-	-	-	-	-	-	23,63	-	-
12	-	-	-	-	-	-	15,53	-	-

Table A24 Mean fortnightly masses* of *B.salinarum* and *B.(P.)africanus*.

Fortnights	*B.salinarum*	*B.(P.)africanus*
1	too small to weigh	too small to weigh
2	0,0251	too small to weigh
3	0,0573	0,1207
4	0,0922	0,2888
5	0,1105	0,4120
6	0,1211	0,4824
7	0,1296	0,5472
8	-	0,5971

*In grams

Table A25 Mean fortnightly masses* of F_2-*B.(B.) tropicus* *B.pfeifferi* and *B.(P.)globosus*.

Fortnights	*B. (B.) tropicus*	*B.pfeifferi*	*B.(P.)globosus*
1	not weighed	not weighed	not weighed
2	0,1016	0.0928	"
3	0,2266	0,1455	0,0046
4	0,2926	0,1672	0,0581
5	0,3320	0,1672	0,1648
6	0,3258	0,1689	0,2416
7	0,3401	0,1704	0,2624
8	-	-	0,2528

*In grams

Table A26 Mean fortnightly masses* of snails being subjected to stepwise increasing and decreasing salinities.

Fortnights	1	2	3	4	5	6	7	8	9	10	11	12
L.natalensis												
250 up	0,0005	0,0377	0,1422	0,1422	0,1863	0,2019	0,2019	-	-	-	-	-
250 down	0,0040	0,1003	0,3826	0,5852	0,5694	0,5237	0,7532	0,8313	0,8969	1,0275	-	
B.pfeifferi												
250 up	0,0215	0,0992	0,1245	0,1768	0,1724	0,1799	0,2049	0,2049	0,2048	0,2099	-	-
250 down	0,0097	0,1054	0,1860	0,2324	0,2454	0,2620	0,2657	0,2761	0,2836	0,3077	0,3362	-
B.(P.) globosus												
250 up	0,0082	0,0758	0,1982	0,2189	0,2508	-	-	-	-	-	-	-
250 down	0,0026	0,0626	0,1889	0,3012	0,3609	0,4252	0,5101	0,5407	0,6009	0,6605	0,6861	0,6861
B.(B.)tropicus												
250 up	0,0076	0,1266	0,2088	0,2414	0,1980	0,2037	0,2037	0,2038	0,2399	0,2340	-	-
250 down	0,0101	0,1187	0,2194	0,2912	0,3891	0,4658	0,5644	0,6617	-	-	-	-

*In grams