AN ORGANIC CARBON ANALYSIS OF THE GROWTH OF *POTAMOPYRGUS JENKINSI* (SMITH) IN RELATION TO TEMPERATURE AND SALINITY.

A thesis submitted for the degree of Doctor of Philosophy

of the University of Stirling.

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(awarded June 1976)

The work presented in this thesis is the result of my own investigations. It has not been, nor will be, submitted for any other degree.

Candidate

Supervisor

1936. Date

ACKNOWLEDGEMENTS

I should like to thank Dr. A. E. Henderson for his advice and criticism throughout this study. I would also like to thank all those people in the Department of Biology at the University of Stirling who have helped me in my studies and Dr. D. Machin of the Department of Mathematics for his advice on statistics.

I must also thank Mr. T. Warwick, of the Department of Zoology : University of Edinburgh, for his help in the identification of different strains of P. jenkinsi and for his general advice on the species.

This work was completed under the tenure of a N.E.R.C. grant.

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by

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Abstract

Potamopyrgus jenkinsi (Smith) is a small gastropod living in freshwater and brackish habitats in Britain. It is currently extending its range in Europe.

This study has involved the elucidation of the growth response of this mollusc to temperature and salinity, in the laboratory. Growth is maximised at $25^{o}C$ and $14^{o}/oo$ salinity.

The method of growth analysis employed was based on the evaluation of the organic carbon content of individual *P. jenkinsi*. The growth rate results are presented in both shell length and carbon terms. The relations between carbon, dry weight and shell length were defined. Variations in these were found with growth conditions. The relation between carbon and shell length is :

$$c = A\, l^{m} \quad (1)$$

This was employed in the linearised form :

$$\log c = m \log l + a \qquad (\text{where } a = \log A - \text{eqn } 1)$$

The overall equation defined for *P. jenkinsi* under all conditions of salinity and temperature (pooled results) was :

$$\log c = 2.3078 \log l + 1.0135$$

The relation of carbon to dry weight was of the form :

$$c = n\,w + b$$

This is a simple linear equation.

(Terms used : c-organic carbon, l-shell length, w-total dry wt., m,n,A,a and b - constants)

The method of organic carbon analysis employed was a small scale development of that used by Russell Hunter et al (1968). In this form the method is ideal for evaluating the biomass of small individual invertebrates. The results in this work demonstrate the high degree of sensitivity and accuracy that can be achieved.

Considerable differences in growth rate resulted from varying temperature and salinity. P. jenkinsi is both eurythermal and eurysaline. Temperature and salinity have been shown to interact synergistically in their effect on growth rates.

The growth of P. jenkinsi is controlled with respect to salinity. No growth regulation was found in relation to temperature : growth rates conformed to the Arrhenius model. There appears to be some endogenous variation in growth potential with the time of year.

The results are discussed in relation to current theories of biochemical and physiological adaptation to the physical and chemical aspects of the environment.

Some consideration is given to the taxonomic state of P. jenkinsi. It is concluded that P. jenkinsi should remain as a single species unit. The species should not be subdivided as suggested by Warwick (1969).

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List of abbreviations used.

a	constant ($\log c = m \log l + a$).
A	constant ($c = Al^m$), $\log A = a$.
b	constant ($c = nw + b$).
c	organic carbon (µg.).
C	log organic carbon.
d.f.	degrees of freedom.
F	variance ratio.
K_e^l	growth rate (exponential) - length based.
K_e^c	" " " - carbon " .
l	shell length (mm.).
L	log shell length.
L	in Appendix I - shell length (mm.).
L/W	" " " - shell length/width ratio.
m	slope coefficient ($\log c = m \log l + a$).
n	" " ($c = nw + b$).
n	number of observations in a sample.
R	∮ for pooled data (total of that from all temp. - salinity combinations).
∮	residual variance.
s	degree of synergistic interaction.
S	sum of.
s.d.	standard deviation.
T	∮ for separate data (specific temp. - salinity combinations).
t	time in days.
w	total dry weight.
W	in Appendix I - total dry weight.
°/oo	salinity - parts per thousand.
°C	temperature - degrees centigrade.

1. Introduction

1.1. General Introduction

Salinity and temperature are important ecological factors. Kinne (1960) has included them in his short list of 'master factors' primarily important in determining the nature of a habitat. Whilst there is a vast literature on the various effects of these environmental parameters, on all aspects of life, there is comparatively little information concerning the effect of simultaneous variation of both factors on physiological processes. This study on the effects of temperature and salinity on the growth of Potamopyrgus jenkinsi (Smith) provides information on the response of a small poikilothermic and euryplastic species in an artificial environment in the laboratory. The ecological implications of the results and the biochemical and physiological mechanisms underlying them are discussed.

1.2. The Species : A Brief Review

P. jenkinsi is a small gastropod widely distributed in Europe. There are a number of papers concerned with the general ecology and physiology of the species : Ellis 1932, Bondesen and Kaiser 1949, Heywood and Edwards 1962, Clay 1967 and Muus 1967. These reveal that P. jenkinsi is a euryplastic species which occurs in all manner of freshwater habitats and in the upper regions of estuaries. Clay's paper includes a more general review of the species as does the work of Fretter and Graham (1962).

Robson (1920) describes the anatomy of the species and Woodward (1892) the radula structure. The distinguishing aspects

of Hydrobiid anatomy and morphology are discussed by Muus (1967) and McLusky (1971).

P. jenkinsi is well known as a parthenogenetic mollusc. Patil (1958) describes the anatomy of the only male that has been found. Robson (1923,26) discusses parthenogenesis in the species in relation to its ecology, distribution and genetics. Sanderson (1940) compares the cytogenetics of parthenogenesis in P. jenkinsi to that of sexual reproduction in Hydrobia (Peringia) ulvae. It is suggested that two races of P. jenkinsi exist : tetraploid in Britain and diploid on the continent. Patterson (1967) suggests that further, more exact, studies be made of the existence of this polyploidy, before it is accepted.

A number of papers discuss the distribution and mode of dispersal of P. jenkinsi (Boycott 1936, Hubendick 1950, Moon 1956, Russell-Hunter, Maitland and Yeoh 1964, Russell-Hunter and Warwick 1957, Heywood and Edwards 1962). The general conclusion is that in Britain P. jenkinsi was spread, first to brackish and then to fresh water habitats by passive dispersal, from an estuarine origin in the Thames, in the late 1800's. Associated with this is the problem of the primary origin of P. jenkinsi as discussed by Bondesen and Kaiser (1949).The existence of a fossil record is proposed by Kennard (1941) and Warwick (1954). The evidence for this is unconvincing (Bondesen and Kaiser 1949). A New Zealand origin for the species has been proposed by Boetteger (1951) and Winterbourne (1970 ab,1972). Winterbourne makes extensive comparisons between P. jenkinsi and Potamopyrgus antipodarum (Gray) from New Zealand, the proposed'ancestor'. This seems to be the most acceptable of the current explanations especially since a good proportion of P. antipodarum are parthenogenetic which is (1) very rare in molluscs and (2) a facet favouring colonization -

perhaps of Europe? Transport by ships into the Thames estuary is certainly consistent with Hubendick's scheme for distribution within Britain, which has, as its centre of dispersion, the Thames, a centre for sea traffic.

The existence of different 'strains' of P. jenkinsi is noted in many papers. Overton (1905), Boycott (1929) and Warwick (1944) investigated the inheritance of the keeled shell in the species. Bondesen and Kaiser (1949) state "that the species has developed ecological races with differences in physiology connected with characteristics in their appearances having value of selection under certain extrinsic factors." Warwick (1952,69) systematised this by proposing the existence of three distinct strains (see Appendix I). A large degree of intraspecific variation, both continuous and discontinuous (polymorphic) would be consistent with what is known of other freshwater molluscs (Diver 1939 ab Russell-Hunter 1970).

The osmotic nature of P. jenkinsi is discussed by Duncan (1967) and Todd (1964). Bryan (1963) used radioactive ions to investigate osmotic and ionic change in this species. P. jenkinsi is basically an osmo-conformer, significantly controlling it s blood concentration only in low salinities and freshwater.

The oxygen consumption of the species is described in four papers (Lumbye 1958, Lumbye and Lumbye 1965, Duncan 1966, Klekowski and Duncan 1966). These describe the respiratory activity of P. jenkinsi under different conditions of temperature, salinity, oxygen concentration and food availability. Duncan's paper is the most important of these since it evaluates the effect of combinations of salinity and temperature on respiration. This author also discusses reproductive activity and survival in relation to salinity.

Thus much is known about P. jenkinsi . This thesis is concerned with the growth of the species.

1.3. Organic Carbon

The growth of P. jenkinsi has been evaluated in terms of both shell length and organic carbon. The latter provides a direct measure of organic biomass. Such a measure is more biologically meaningful than conventional shell size or total weight measurements (Russell-Hunter et al 1968). The variation in the morphology of the shell of P. jenkinsi (Appendix I) makes the use of organic carbon analysis necessary since the comparison of the growth of such varying animals in terms of linear dimensions is necessarily simplistic.

The population used as a source of material for the experiments is composed of only one of Warwick's types. Even within this apparently homogenous population there was some variation in shell shape, possibly reflecting, at least under some conditions, differences in organic biomass and the shell length - total weight relation.

The method of organic carbon analysis employed in this work is a small scale development of the 'wet oxidation' procedure employed by Russell-Hunter et al (1968). The advantage of using organic carbon, as an evaluation of growth, is similar to that confered by calorific value : the result is objective and comparable. However, organic carbon analysis is more rapid and easily repeated than bomb calorimetry : vital where large numbers of animals are involved. Further, the scale of the method may be tailored to the size of the animal being investigated. Thus accuracy is maximised.

The main disadvantage of organic carbon analysis, which is shared with the other useful measures of biomass, dry weight and calorific value, is that the animal must be killed. Thus it cannot be directly employed in continuing growth studies on specific animals. Organic carbon can be related by regression to the non-destructive

measures of growth used in such work.

The following section (2) deals with the elucidation of the 'allometric' relations between length, dry weight and organic carbon. Variation in these relations due to temperature and salinity are investigated. The results are employed in the chapter on growth studies (3) where 'length - growth' is converted to'carbon - growth'.

2. Organic Carbon Analysis

2.1. Introduction to the Method

As stated, the procedure is based on that of Russell-Hunter et al (1968). Preliminary work suggested that the largest individual adult P. jenkinsi would contain less than 700 µg. of organic carbon. It was also shown that the smallest size of animal to be used ; juveniles about 1.0 mm. in length, had a minimum organic carbon content of about 6.0 µg. Thus it was necesary to design an accurate experimental technique to cover the range 6.0 - 700 µg. of organic carbon. At all times animals were analysed individually since this must enhance accuracy when using such a sensitive method, responsive to small differences in the carbon input.

The 'micro - level' experiment, described by Russell-Hunter et al (1968), employing 10 ml. of the standard chromic acid oxidizing agent, gives a range of 125 µg - 2.5 mg. of organic carbon. This was too cumbersome and did not cover the required range. Thus the amount of oxidant had to be reduced in order to increase sensitivity. Eventually, following a period of trial and error, it was decided to develope three ' sub - micro' levels of analysis, employing different volumes of chromic acid :

(1) 4ml. acid : range 50 - 1000 µg. organic carbon
Used on adult P. jenkinsi of 4.0 mm. + in shell length.

(2) 2ml. acid : range 25 - 500 µg. organic carbon
Used on middle sized P. jenkinsi : shell length 2.0-4.0 mm.

(3) 0.5ml. acid : range 6.5 - 125 µg. organic carbon

Used on small P. jenkinsi : generally less than 2.0 mm. in shell length.

It can be seen that there is a considerable 'carbon overlap' between these three procedures. This gives flexibility so that a size of animal that might be considered intermediate between two treatments may be dealt with using either the smaller or larger scale procedure.

During the development of the method glass pipettes were found to be totally inadequate in relation to the demands placed on them. Chromic acid is very viscous, highly corrosive and liberates considerable amounts of heat during hydration. These properties made the use of ordinary pipettes and small volume constriction pipettes untenable since they were difficult to use and clean and often proved inaccurate. Thus Ependorf automatic pipettes with disposable inert plastic tips were used to dispense the oxidant.

At all times extreme care was taken over the cleanliness of apparatus and accuracy of technique. As Russell-Hunter et al (1968) state "a single fingerprint has a detectable organic carbon content." The method employed here was much more sensitive to error due to the smaller volumes of oxidant and amounts of carbon involved. At all times large volumes of standard solutions were produced in order minimise the effect of errors.

2.2. Method

(a) The Animals. The primary aim of these experiments was to define the (allometric) relation between shell length and organic carbon under the same conditions of salinity and temperature used

in the growth experiments. Large samples of P. jenkinsi were taken from the River Ore at Thorton in Fife. Animals varying in length between 0.5 and 1.2 mm. were selected for carbon analysis. These animals were maintained as stock'populations'at all combinations of 5,10,15,25 and 30 °C and 0,3.5,7,14,21 and 28°/oo salinity. Due to the very large numbers of animals involved they could not all be kept individually.Usually they were maintained and grown three or four per 100 ml. of water in small plastic containers. Excess food was supplied (Oak leaves). No adverse effects of crowding were observed. Simpson (1975) showed that crowding reduced the growth and natality of P. jenkinsi.

The animals were analysed for organic carbon only after 3 - 4 weeks in the specific temperature - salinity medium to which they had been allocated. Most of the animals were maintained for longer, only those being used to determine the carbon content of very small animals being used after such a short period of adjustment to the specific test conditions. By allowing the animals to grow for different periods of time a range of sizes could be analysed.

When the animals from the growth experiments (section 3) reached full size these were also subjected to organic carbon analysis. The use of these'growth animals' in the length - carbon regressions maximised the association of the 'allometric' and growth experiments. No anomalous differences were observed between the carbon values of the individually maintained animals from the growth experiments and those of the others kept in groups of three or four (Fig 4).

(b) Experimental Procedure. The chromic acid oxidant was made in two - litre batches. It was prepared by dissolving 9.68 g. of analytical grade potassium dichromate in 40 ml. of warm distilled water in a two litre pyrex beaker. This was allowed to partially cool and then about a litre of analar grade concentrated sulphuric

acid was very gradually added. This must be done with great care since large quantities of heat are liberated. This was left to cool, transferred to a two litre volumetric flask and made up to volume with more concentrated sulphuric acid. The solution must be thoroughly mixed prior to use. At all times great care must be taken for personal protection from this corrosive material, whilst it is ensured that no contamination occurs. The oxidant was kept for up to three months in a dark cupboard in glass stoppered bottles. After this time the accumulated effects of exposure to light alter the colour of the solution to a less bright brown. This was then seconded for acid-cleaning glassware whilst a new batch was made for experiments.

The analysis is calibrated using glucose - carbon standards. This was frequently checked and always repeated when a new batch of acid was introduced. The basic carbon standards were made as in the original method (Russell-Hunter et al 1968). 7.5g. of anhydrous dextrose was disolved in 100ml. of distilled water giving a concentrated solution (30 mg. org. c. ml^{-1}) which could be stored in a refrigerator for a week. Various dilutions were made from this in order to provide suitable ranges of carbon for the calibration of each of the three scales of experiment. The calibration lines are straight within the stated ranges of the experiments.

For calibration 0.5 ml. of a standard carbon solution was added to either 0.5, 2 or 4 ml. of chromic acid, depending on the experiment, in small test tubes. Blanks and experiments analysing the carbon content of animals had 0.5 ml. of distilled water added to the acid. Foil caps were placed on the test tubes to minimise contamination. The animals were always analysed individually : one per tube.

The tubes were placed in a block heater at $105^{o}C$ for one hour. They were then allowed to cool and the acid solution decanted

into volumetric flasks, great care being taken to wash all of the solution out of the tubes. The 0.5 and 2ml. scale solutions were made up to 5 ml. with distilled water, whilst the solutions based on 4 ml. of acid were made up to 10 ml. Since this liberated heat, bringing the solutions to the exact volume was left until they had returned to room temperature.

The optical density of the test solutions was found using a Pye Unicam SP 1800 split beam spectrophotometer. This simplifies the taking of readings since the blank is optically dense compared to the test solutions. Single beam machines require that the experimenter zeroes the machine on each test solution and reads the denser blank against it. With a split beam instrument the normal position of the blank and test solution is merely reversed and the usual procedure followed. Animal carbon values were found by reading their absorption value on the relevant carbon - absorption calibration curve.

The presence of carbon in the chromic acid can be discerned by the presence of a greenish yellow colour as opposed to the orange - brown of unreacted chromic acid. A strong emerald green or black colour is an immediate indication that the acid has been overloaded with carbon into the non - linear phase of absorption change.

2.3. Results

Table 24 in Appendix II contains the data concerning individual animals : length, log length, wet weight, dry weight, organic carbon and log organic carbon. This basic data was used in the calculation of the regressions :

(1) $\log c = m \log l + a$

(2) $c = n w + b$

where m, n, b and a are constants ($a = \log A$ - equation 3)

c - organic carbon

w - dry weight

l - shell length

Equation (1) may be expressed as below :

$$(3) \qquad c = A\, l^{m}$$

This is the well known expression used in the study of allometric growth relations (Wilbur and Owen 1964, Weatherley 1972). Equation (2) is an example of this type of expression where the power is unity. The relation between carbon and dry weight may be described as isometric since the relation is of a constant type which does not change with growth. The numerical ratio between shell length and organic carbon content is variable since m is not unity (Table 1).

The regressions (equations 1 and 2) for each combination of temperature and salinity are presented in Tables 1 and 2. In all cases highly significant correlations were found. The high degree of accuracy of these regressions must in part be due to the consistent use of data concerning individual animals. For each animal the length, weight and organic carbon were separately determined. Mean values were not employed.

Figs 1-3 show the relations between organic carbon, dry wt. and shell length. There are considerable differences in the regressions (constants) presented in Tables 1 and 2, depending on the conditions under which the animals were grown. Figs 1-3 are graphs employing data based on animals grown at 7°/oo salinity and 15°C. Fig 1 shows the regression of organic carbon content on dry wt. This is a simple linear plot (see eqn. 2). Fig 2 is a presentation of the relationship between log l and log dry wt. This double log relation gives a linear plot (fitted by eye). Fig 3 is an example of the log c vs. log l regressions

Table 1

The relation between organic carbon and shell length determined under different conditions of temperature and salinity. Regressions : $\log c = m \log l + a$.

c = organic carbon, µg.

l = shell length, mm.

m and a are the constants for a single set of conditions.

Salinity	Temperature	Regression Equations	Correlation Coefficient	Significance
0°/oo	5°C	log c = 2.7957 log l + 0.9246	0.9838	99%
	10°C	log c = 2.5370 log l + 0.8786	0.9249	99%
	15°C	log c = 2.3622 log l + 0.9163	0.9763	99%
	25°C	log c = 2.5348 log l + 0.8650	0.9604	99%
	30°C	log c = 1.9414 log l + 1.1042	0.9502	99%
3.5°/oo	10°C	log c = 2.3174 log l + 1.1044	0.9973	99%
	15°C	log c = 2.2280 log l + 1.1183	0.9943	99%
	25°C	log c = 2.2015 log l + 1.0993	0.9909	99%
	30°C	log c = 2.0536 log l + 1.0657	0.8899	99%
7°/oo	5°C	log c = 2.6410 log l + 1.0353	0.9527	99%
	10°C	log c = 2.4180 log l + 0.9672	0.9939	99%
	15°C	log c = 2.1526 log l + 1.0785	0.9803	99%
	25°C	log c = 2.3564 log l + 1.0054	0.9882	99%
	30°C	log c = 2.5813 log l + 0.8320	0.9712	99%

Salinity	Temperature	Regression Equations	Correlation Coefficient	Significance
14°/oo	5°C	log c = 2.7797 log 1 + 0.9795	0.9537	99%
	10°C	log c = 2.4722 log 1 + 0.9636	0.9916	99%
	15°C	log c = 2.3279 log 1 + 0.9836	0.9926	99%
	25°C	log c = 2.3668 log 1 + 0.9751	0.9909	99%
	30°C	log c = 2.2777 log 1 + 0.9940	0.9940	99%
21°/oo	5°C	log c = 1.9766 log 1 + 1.2188	0.9505	99%
	10°C	log c = 2.3661 log 1 + 0.9962	0.9923	99%
	15°C	log c = 2.3636 log 1 + 0.9445	0.9871	99%
	25°C	log c = 2.4478 log 1 + 0.8961	0.9886	99%
	30°C	log c = 2.4440 log 1 + 0.9134	0.9606	99%
28°/oo	5°C	log c = 2.2982 log 1 + 1.2027	0.8952	99%
	10°C	log c = 1.9105 log 1 + 1.2761	0.9753	99%
	15°C	log c = 1.9826 log 1 + 1.1630	0.9609	99%
	25°C	log c = 1.3973 log 1 + 1.2025	0.7503	90%
	30°C	log c = 1.1016 log 1 + 1.5383	0.9048	99%

Table 2

The relation between organic carbon and dry wt., determined under different conditions of temperature and salinity. Regressions : $c = n\,w + b$

c = organic carbon, µg.

w = dry wt., mg.

n and b are the constants for a single set of conditions.

Salinity	Temperature	Regression Equations	Correlation Coefficient	Significance
0°/oo	5°C	c = 127.0960 w - 8.5327	0.9624	99%
	10°C	c = 126.8847 w - 28.1372	0.9778	99%
	15°C	c = 94.2339 w + 0.4439	0.9598	99%
	25°C	c = 103.1158 w + 2.9963	0.9813	99%
	30°C	c = 67.0114 w + 15.2211	0.8417	99%
3.5°/oo	10°C	c = 129.3837 w - 10.5188	0.9948	99%
	15°C	c = 116.7002 w + 3.1103	0.9514	99%
	25°C	c = 98.1045 w + 5.4300	0.9774	99%
	30°C	c = 64.1475 w + 17.6998	0.9087	99%
7°/oo	5°C	c = 133.6180 w + 6.4456	0.9725	99%
	10°C	c = 123.6960 w + 21.9801	0.9831	99%
	15°C	c = 100.0985 w + 3.9209	0.9868	99%
	25°C	c = 105.7735 w + 2.6229	0.9875	99%
	30°C	c = 91.2785 w + 13.9591	0.9059	99%

Salinity	Temperature	Regression Equations	Correlation Coefficient	Significance
14°/oo	5°C	c = 133.0790 w + 4.8467	0.9912	99%
	10°C	c = 118.0202 w + 7.2833	0.9898	99%
	15°C	c = 94.2809 w + 24.8780	0.8868	99%
	25°C	c = 102.7416 w + 1.3846	0.9859	99%
	30°C	c = 104.1492 w + 0.2040	0.9805	99%
21°/oo	5°C	c = 106.2070 w + 3.8314	0.9493	99%
	10°C	c = 113.6847 w + 0.2301	0.9914	99%
	15°C	c = 111.9810 w + 19.2580	0.9766	99%
	25°C	c = 98.0350 w + 0.4228	0.9943	99%
	30°C	c = 84.2798 w + 6.0036	0.9174	99%
28°/oo	5°C	c = 122.0754 w + 0.1861	0.9523	99%
	10°C	c = 114.5059 w + 6.3166	0.9825	99%
	15°C	c = 100.3752 w + 2.5964	0.9849	99%
	25°C	c = 61.0209 w + 9.8637	0.7533	90%
	30°C	c = 71.4691 w + 26.6314	0.9048	99%

Figure 1

An example of the regression $c = n\,w + b$

produced using animals grown at $15^{\circ}C$ and $7^{\circ}/oo$ salinity.

+ b

alinity.

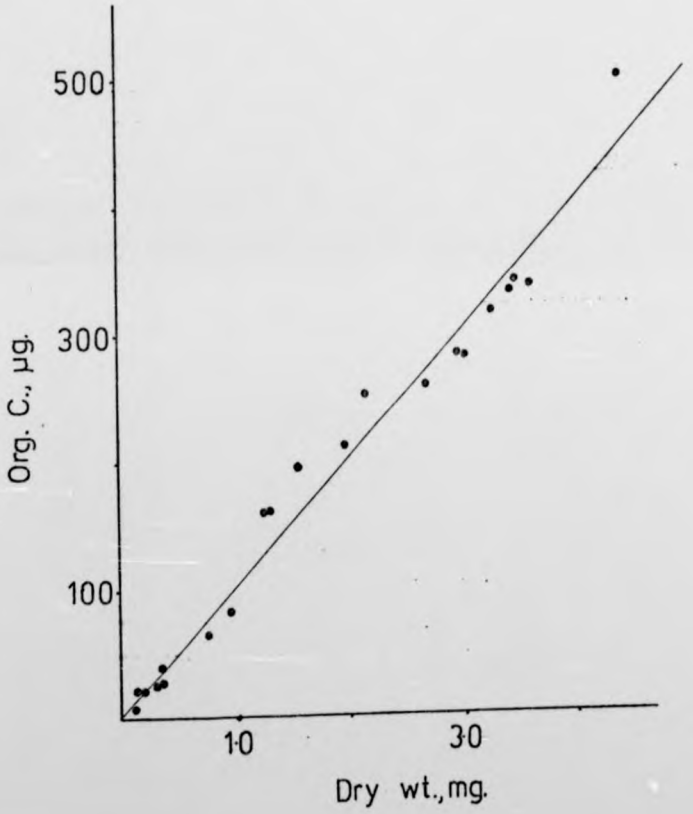


Figure 2

The relation between log l and log w (fitted by eye) for animals grown at 15°C and 7°/oo salinity.

l = shell length.

w = dry wt.

(see Calow 1975)

fitted by

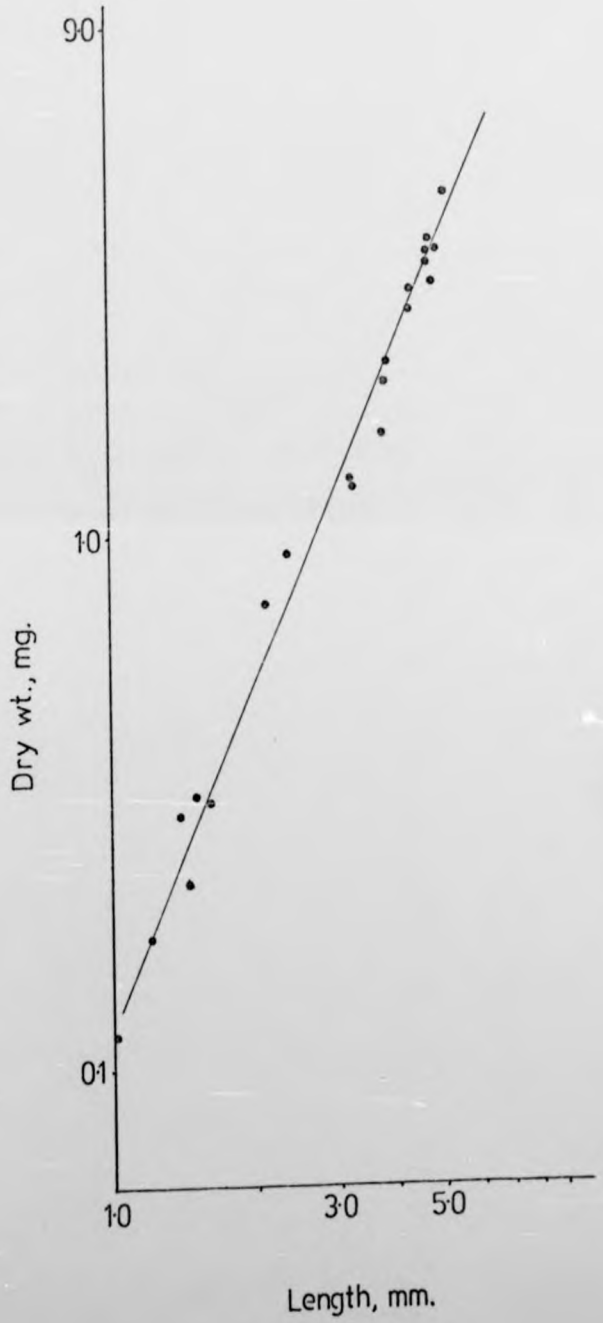
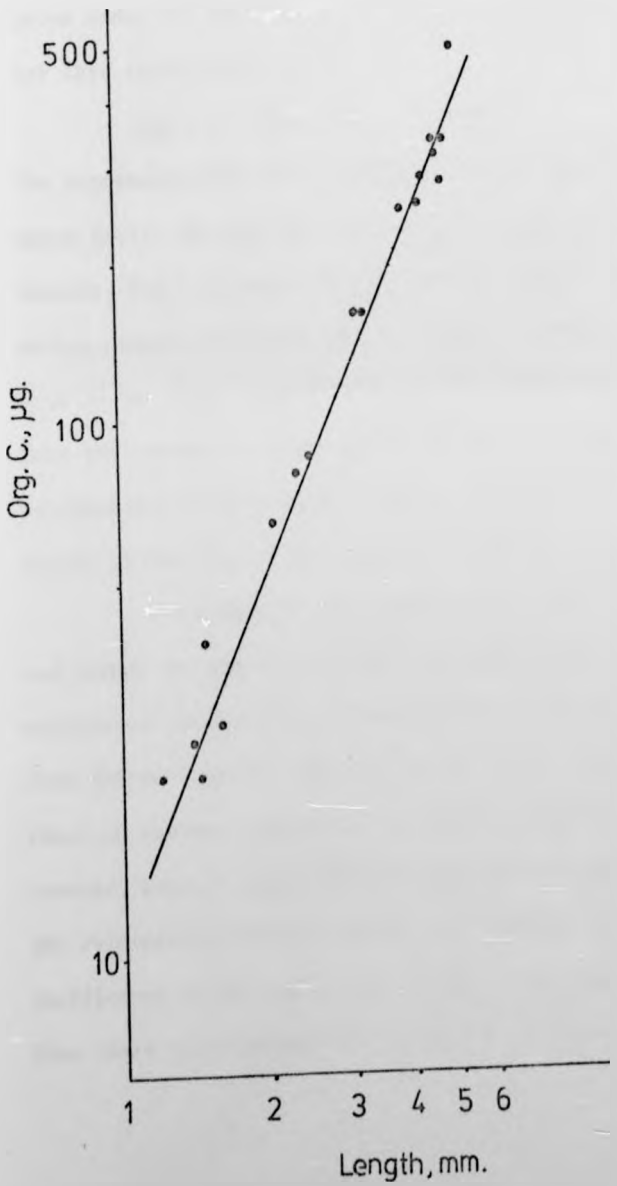


Figure 3

An example of the regression $\log c = m \log l + a$ produced using animals grown at $15^{\circ}C$ and $7^{\circ}/oo$ salinity.

m log l + a

alinity.



used to convert growth data based on shell length to carbon based terms. These regressions are linear.

Fig 4 is a similar plot to Fig 3 except that it is based on all the shell length - organic carbon data from animals grown under all conditions of salinity and temperature. The equation for this relationship is :

$$\log c = 2.3078 \log l + 1.0135.$$

The regression line is a significant fit at the 99% level. As is shown later, the pooling of this data is statistically invalid. However, Fig 4 illustrates the general relation between organic carbon content and shell length. Fig 5 is a direct plot of the data in the form shown in equation (3). The curve is generated from the regression equation for Fig 4. Fig 5 shows how the relationship between organic carbon content and shell length varies as the size of the animal increases.

The slopes of the regressions of log c vs. log l and carbon vs. dry wt.,are shown in temperature - salinity matrices,in Tables 3 and 4 respectively. These values are taken from Tables 1 and 2. The log c vs. log l data in Table 3 shows no obvious temperature or salinity related trends. However, Table 4 shows definite temperature dependent trends in the relationship between dry wt. and organic carbon. The slope coefficient of the regression declines with increasing temperature. Thus there is a tendency for an animal at agiven dry wt. to contain more

Figure 4

Total pooled data plot of the regression ; $\log c = m \log l + a$. Produced using animals from all conditions of temperature and salinity.

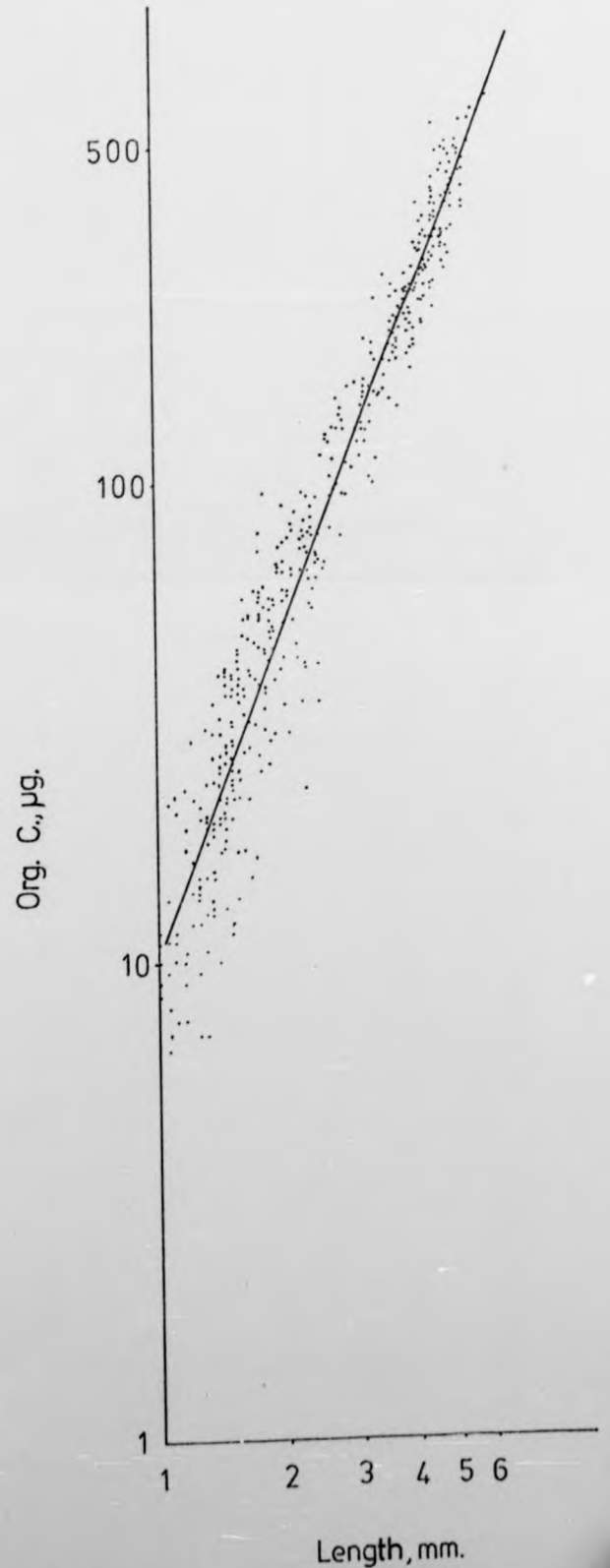

500
100
10
1
Org. C, µg.
1
2
3
4
5
6
Length, mm.

Figure 5

Presentation of the curve $c = A\,l^m$ (page 11).

This was derived from Fig 4 (the data).

c = organic carbon, µg.

l = shell length, mm.

A and m are constants

11).

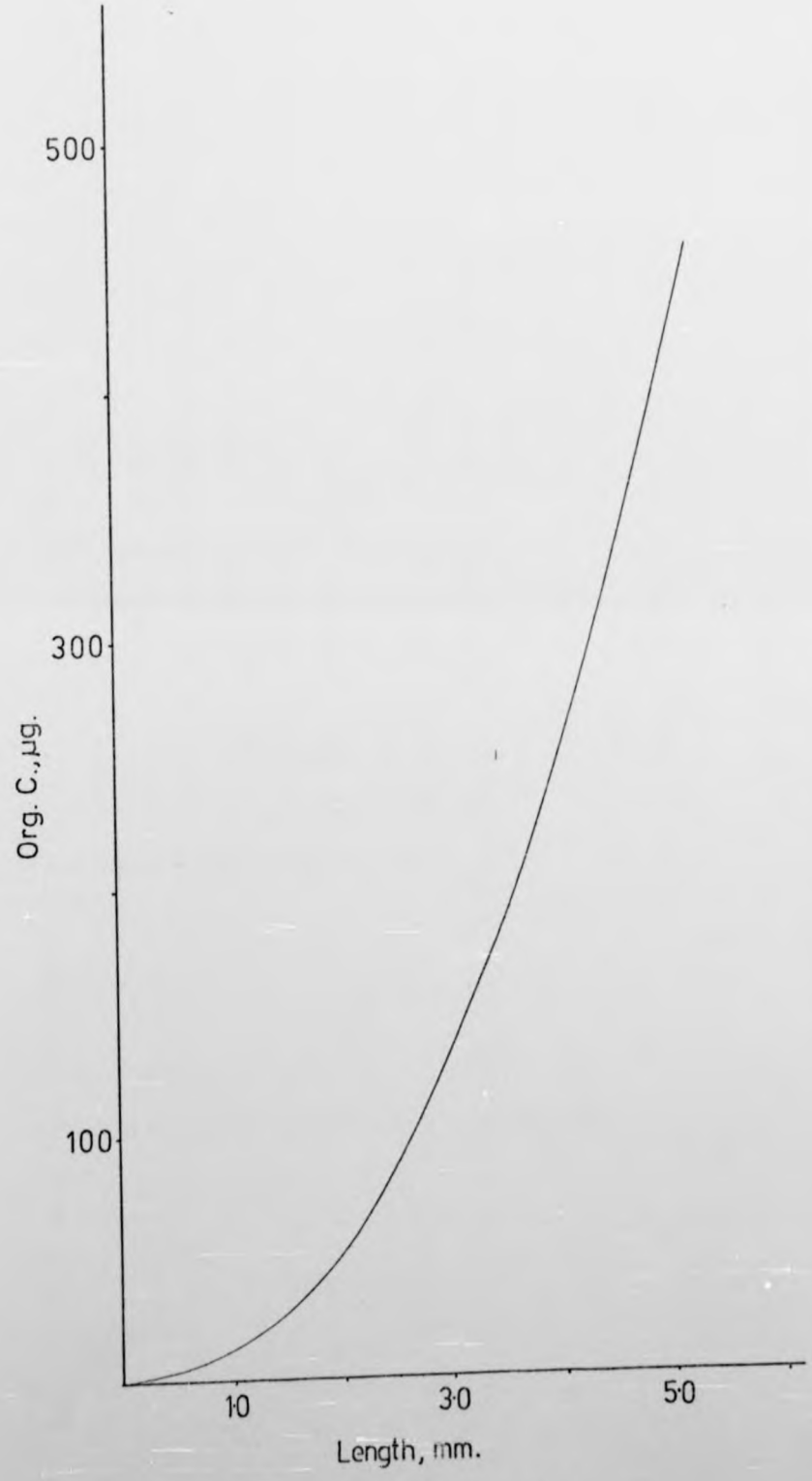


Table 3

Values of the slope coefficient m ($\log c = m \log l + a$) presented in a matrix of salinity and temperature.

c = organic carbon, ug.

l = shell length, mm.

m and a are constants for a single set of conditions.

Table 4

Values of the slope coefficient n ($c = n w + b$) presented in a matrix of salinity and temperature.

c = organic carbon, ug.

w = dry wt.

n and b are constants for a single set of conditions.

	Salinity °/oo	Temperature °C : 5	10	15	25	30
Table 3	0	2.7957	2.5390	2.3622	2.5348	1.9414
	3.5	----	2.3174	2.2280	2.2015	2.0536
	7	2.6410	2.4180	2.1526	2.3564	2.5813
	14	2.7797	2.4722	2.3279	2.3668	2.2777
	21	1.9766	2.3661	2.3636	2.4478	2.4440
	28	2.2982	1.9105	1.9826	----	----
Table 4	0	127.0960	126.8827	94.2339	103.1158	67.0114
	3.5	----	129.3837	116.7002	98.1045	64.1475
	7	133.6180	123.6960	100.0985	105.7735	91.2785
	14	133.0790	118.0202	94.2809	102.7416	104.1492
	21	106.2070	113.6847	111.9810	98.0350	84.2798
	28	122.0754	114.5091	100.3752	61.0209	71.4691

Table 5

Correlation coefficients for the relationship

between temperature and the slope coefficient n($c = nw + b$).

onship

= nw + b).

Salinity °/oo	Correlation Coefficient	Significance
0	0.8699	sig. at the 98 % level
3.5	0.9595	" " " 99 % "
7	0.8835	" " " 98 % "
14	0.6891	not " " " 90 % "
21	0.8296	" " " 95 % "
28	0.9493	" " " 99 % "

organic carbon if grown under colder conditions.

Table 5 shows the correlation coefficients and their significance levels for the relation between temperature and the slope coefficient n ($c = nw + b$). In all salinities except $14^{o}/oo$ the correlation is highly significant.

Statistical Treatment. It was deemed necesary to test whether a significant single line could be fitted to all of the data forming the separate log carbon - log length regressions produced under different conditions of temperature and salinity. Such a single line would simplify and standardise the conversion of growth data in length terms to carbon. The pooled data line is presented in Fig 4. This may be compared to Fig 3 which is the regression for only one combination of salinity and temperature.

For each separate line and for the total pooled data line, $\not$ residual was calculated :

$$\not = S (C - \bar{C})^2 - m^2 \; S (L - \bar{L})^2$$

$$\not = \left\{ SC^2 - \frac{(SC)^2}{n} \right\} - m^2 \left\{ SL^2 - \frac{(SL)^2}{n} \right\}$$

where $\not$ - residual variance, m - slope coeff.

C - log carbon, L - log length

n - number of observations

S - sum of

These values of $\not$ residual are presented in Table 7 whilst the basic sums of squares data may be found in Table 6.

The significance of the difference between $\not$ residual for the pooled data line and the $\not$ residual values for all the separate lines was analysed by F test.

Table 6

Statistical (sums of squares) data for the comparison of the separate $\log c = m \log l + a$., regressions to that of the total pooled line.

S = sum of.

C = log c.

L = log l.

n = the number of observations.

m and a = regression constants.

Conditions		S LC	S C^2	S C	S L^2	S L	n	m	a
0°/oo	5°C	4.8684	32.3689	20.2614	0.7664	2.9480	13	2.7957	0.9246
	10	38.2071	184.8854	97.7563	8.4320	19.1367	56	2.5370	0.8786
	15	13.4844	57.3252	27.7402	3.2597	6.3126	14	2.3622	0.9163
	25	12.5642	58.2057	29.9992	2.8977	6.0337	17	2.5348	0.8650
	30	9.2385	48.1285	27.1688	1.9750	4.8944	16	1.9414	1.1042
3.5	10	8.5929	40.5083	18.6382	1.9191	3.7534	9	2.3174	1.1044
	15	15.5167	66.7146	28.7104	3.7716	6.3613	13	2.2280	1.1183
	25	22.3744	91.8699	38.7034	5.6234	9.0921	17	2.2015	1.0993
	30	5.3343	27.6493	15.4278	1.1228	2.8412	9	2.0536	1.0659
7	5	5.0375	36.4178	22.2247	0.7599	2.9272	14	2.6410	1.0353
	10	20.0415	94.4705	47.4726	4.5953	9.2331	26	2.4180	0.9672
	15	22.2069	94.5822	43.2956	5.5167	9.5915	21	2.1526	1.0785
	25	22.1571	94.3401	41.7322	5.4875	9.1766	20	2.3564	1.0054
	30	16.9418	72.9472	34.7018	4.1002	7.6418	18	2.5813	0.8320

Conditions		S LC	S C^2	S C	S L^2	S L	n	m	a
14°/oo	5°C	7.1586	45.1230	25.6263	1.1893	3.9331	15	2.7797	0.9795
	10	22.0888	106.9493	54.1596	4.9536	10.2143	30	2.4722	0.9636
	15	19.1707	83.3820	39.3079	4.6712	8.4351	20	2.3279	0.9836
	25	21.1530	89.3652	40.1430	5.3440	8.7000	20	2.3668	0.9751
	30	16.5424	71.3459	33.6798	4.0474	7.3678	17	2.2777	0.9940
21	5	3.3140	29.2475	18.5856	0.4413	2.0033	12	1.9766	1.2188
	10	14.9922	72.8771	37.4527	3.3944	6.9872	21	2.3661	0.9962
	15	16.1450	66.4385	29.8647	4.0171	7.0406	14	2.3636	0.9445
	25	18.0265	76.1396	35.4787	4.6047	7.5386	19	2.4478	0.8961
	30	14.5398	68.6577	35.9132	3.2509	7.2204	20	2.4440	0.9134
28	5	1.7485	18.6529	12.1188	0.1922	1.0866	8	2.2982	1.2027
	10	9.1277	53.3284	28.0970	1.6468	4.6871	15	1.9105	1.2761
	15	11.8649	57.1244	28.7612	2.6364	5.7077	15	1.9826	1.1630
	25	insufficient data							
	30	"	"						
Total data		392.44	1839.0751	913.0211	90.6166	180.8654	489	2.3078	1.0135

Table 7

Values of χ residual for the regressions :

$\log c = m \log l + a$.

Conditions		ϕ (residual variance)
Total pooled data - all conditions		8.0243
0°/oo	5°C	0.0249
	10	2.0564
	15	0.0534
	25	0.4086
	30	0.1937
3.5°/oo	10°C	0.0102
	15	0.0376
	25	0.0682
	30	0.2503
7°/oo	5°C	0.1050
	10	0.0951
	15	0.0565
	25	0.1706
	30	0.3435
14°/oo	5°C	0.1217
	10	0.1536
	15	0.0911
	25	0.1706
	30	0.3435
21°/oo	5°C	0.0445
	10	0.0936
	15	0.0698
	25	0.2220
	30	0.3219
28°/oo	5°C	0.0631
	10	0.0340
	15	0.1515
	25	insufficient data
	30	" "
Sum of separate line data		5.4863

Pooled data line $\not$ = R = 8.0243

d.f. = 488

Sum of $\not$ for separate lines = T = 5.4863

d.f. = 433

$$F = \frac{R - T}{488-433} \Big/ \frac{T}{433}$$

This is distributed as F (55, 433) d.f.

F = 3.6299

This is significant. Therefore the pooled line must be rejected.

Thus since the pooledline is statistically invalid due to the existence of'real'variation in the data (related to the treatments) it was decided to employ the separate log carbon - log length regressions in the conversion of the length growth data to carbon growth terms.

3. Growth Studies

3.1. Introduction

The growth experiments are based on the consecutive measurement of individuals. Maintaining animals individually has the advantage of eliminating intraspecific interactions. The importance and nature of such interactions in a given situation is generally unclear and completely unknown for P. jenkinsi. Evidence concerning chemical interaction in a number of species has been produced (Turner 1926,27 , Chernin and Michelson 1957 III and IV, Wright 1960, Berrie and Visser 1963).

Isolating the animals also confers the advantage that any (given) results may be interpreted with more precision since the individuals are identifiable. This approach simplifies the investigation of the causes of anomalous growth performance. In fact the results were reasonably homogenous within each set of conditions, an acceptable degree of individual variation being manifest. Thus individual growth data are not presented. The mean growth of sets of animals is recorded with the standard deviation.

The growth of the animals was followed using shell length. The mean growth rates in terms of length were calculated and these were converted to carbon rates using the allometric length - carbon regressions produced in section 2.

3.2. Methods : General Description

The animals used in these experiments were taken from the River Ore at Thornton in Fife. Mr. T. Warwick has confirmed that this is a homogenous population conforming to his strain A P. jenkinsi (Warwick 1952,69).The snails were grown individually in about 100 ml. of water in push - top plastic containers. This left approximately 50 ml. of airspace in each container. The fitting of the lids was sufficiently tight to prevent evapo ration and maintain constant salinities.

Each snail was supplied with a reasonably standard excess quantity of 'weathered' Oak leaves from Airthrey loch (3-4 leaves depending on size)(see Hanlon 1974). The freshwater was also taken from the loch whilst the sea water came from the university aquarium.

Large numbers of animals were used in these experiments but despite the difficulties imposed by this each growth experiment was started on a certain day using animals removed from the river within a week of the starting date.For the period prior to an experiment the animals were kept in large surgical trays containing Oak leaves and freshwater, at a temperature of 10 ^{o}C. All the range of salinities used in an experiment were made up on the starting day using water taken at that time. The food - leaves were collected at the same time as the fresh water and washed clean of organisms and detritus. Thus within each experiment the conditions were reasonably homogenous and the animals were treated in precisely the same manner except for the controlled experimental variables : temperature and salinity.

P. jenkinsi were maintained at 5,10,15,25 and 30^{o}C and 0,7,14,21 and 28^{o}/oo salinity. In the two major experiments (2 and 3)

Table 8

An explanatory table showing the organisation of growth experiments 1 - 4.

January 1974 - animals - Growth expt.(1) $10^{o}C$ x 0,4,8,16$^{o}/_{oo}$

↓

A success - develop and expand

↓

July 1974 - animals - Growth expt.(2a) 0,5,10,15,25,30^{o}C x 0,7,14,21,28$^{o}/_{oo}$

↓

Poor growth - Growth expt.(2b) - test cold exposure - $15^{o}C$ x 0,7,14,21,28$^{o}/_{oo}$

↓

Repeat

↓

December 1974- animals - Growth expt.(3) 0,5,10,15,25,30^{o}C x 0,7,14,21,28 @ 3.5$^{o}/_{oo}$

↓

Rapid growth

↓

Therefore compare food and water from expts. 2a and 3

↓

April 1975 - animals - Growth expt.(4) $25^{o}C$ x 7 and 14$^{o}/_{oo}$

Growth in freshly made saline water compared to performance in July and December previously used experimental water - from expts. 2a @ 3.

ten individually maintained snails were kept at each combination of the above salinities and temperatures. In the other experiments ten animals were used in each set of conditions employed, except where different numbers are noted. In all of the experiments the snails were maintained in the dark. This was both technically easier than maintaining a day / night regime and biologically reasonable since P. jenkinsi very often live in deep mud, detritus, or under stones, where illumination is minimal. The temperatures 5, 10 and 15°C were maintained in constant temperature rooms whilst 25 and 30°C were achieved using incubators.

The shell lengths of the snails were measured regularly. The animals were removed from their containers and rapidly measured using a dissecting microscope at approximately 20x magnification with a calibrated eyepiece graticule. During the measurement the lids were left off the containers so that the air in them was freshened. At no time was any sign of anaerobiosis observed.

3.3. The Experiments (Methods)

Growth experiment (1). A preliminary experiment was started in January 1974. This was successful and involved the growth of P. jenkinsi at 10°C and 0, 4, 8 and 16°/oo salinity.

Growth Experiment (2a). As a result of the success of the previous experiment a large and comprehensive growth experiment was started in July 1974. There were ten snails at each combination of 5, 10, 15, 25 and 30°C and 0, 7, 14, 21 and 28°/oo salinity. The growth of these animals was suppressed by comparison with that of the animals

in experiment (1).

Growth experiment (2b). Some animals from experiment (2a); those growing at 15°C, were placed at 5°C for five weeks. They were then returned to 15°C. This was an attempt to show whether cold exposure, as experieced in winter, might affect the growth of these 'summer animals'.

Growth experiment (3). This was essentially a repeat of experiment (2a). It was however more successful the animals achieving rapid rates of growth. In January 1975 some animals were started growing at 3.5°/oo salinity. Whilst not strictly comparable to the rest of experiment (3) the results from this fill a gap in the data for the lower salinity range.

Growth experiment (4). This final growth experiment was performed in order to compare the July and December growth experiments (2a and 3 respectively) which displayed disparate results. The animals were grown at 25°C and either 7 or 14°/oo. The animals were freshly collected in April 1975 and placed in (a) water previously used to grow the animals taken in July 1974 (that used in experiment 2a), (b) freshly made - up saline water and (c) water from experiment (3) : that used to grow the animals taken in December 1974. Those animals growing in the previously used water from experiments (2a) and (3) were also given food - leaves from them.

Assuming that there is some seasonal variation in growth potential the animals in freshly made up water should have provided a control for the 'standard April growth rate'. The growth of the other animals could be compared with this and the effects of differences in food, water or the conditioning of the media, detected.

Smaller numbers of animals were used in this experiment due to the restricted quantities of water remaining from experiments (2a) and (3).

3.4. Results

Tables 9 - 13 show considerable variation in the growth of P. jenkinsi between experiments started at different times of the year. These differences may be attributed either to some seasonal effect on the species growth potential or to some experimental variation involving food or water quality.

Growth experiment (1) The growth of P. jenkinsi in this preliminary experiment was deemed sufficiently vigorous and 'healthy' to justify basing larger, more comprehensive, experiments on the same approach (Table 9). The animals achieved 'good' final sizes (4 mm.+) and reasonable rates of growth under all the conditions tested.

Growth experiment (2a) This larger comprehensive salinity - temperature growth experiment was started in July 1974 following the success of the preliminary experiment. Unfortunately growth was generally suppressed and it is difficult to draw useful conclusions about the effects of salinity and temperature. The results are shown in Table 10 and comparison with Tables 9 and 12 illustrates this poor growth.

Growth experiment (2b) Cold exposure for five weeks did not increase the growth rates of these 'summer taken' P. jenkinsi from experiment (2a). When returned to 15°C their growth remained similar to the pre - treatment rate (Table 11). Five weeks may have been an insufficient period or 5°C too warm.

Table 9

Results of growth experiment (1). The mean lengths of batches of ten animals are shown. The time at which the measurements were taken is presented in days, day 0 being the starting day.

Table 9

Results of growth experiment (1). The mean lengths of batches of ten animals are shown. The time at which the measurements were taken is presented in days, day 0 being the starting day.

mean lengths

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y 0 being

Time, days	0	37	79	126	162
10°C, 0°/oo	1.05	1.75	2.9	3.8	4.2
10°C, 4°/oo	0.99	2.13	3.9	4.6	4.9
10°C, 8°/oo	1.09	1.6	2.9	3.9	4.3
10°C, 16°/oo	1.08	1.4	3.2	4.0	4.4

Table 10

Results of growth experiment 2a. The mean lengths and standard deviations of sets of ten animals, each set growing under different conditions of salinity and temperature, are shown. The times of the measurements, in days, are presented.

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rature, are shown.

nted.

Time, days	: 0	43	68
5°C, 0°/oo			
mean l	: 0.99	1.15	1.34
s.d.	: 0.14	0.18	0.21
5°C, 7°/oo	:		
mean l	: 0.94	1.02	1.21
s.d.	: 0.17	0.22	0.32
5°C, 14°/oo	:		
mean l	: 1.05	1.11	1.21
s.d.	: 0.18	0.17	0.15
5°C, 21°/oo	:		
mean l	:0.93	1.0	1.05
s.d.	: 0.16	0.23	0.27
5°C, 28°/oo	:		
mean l	: 0.90	0.91	0.92
s.d.	: 0.08	0.08	0.07

Time, days	: 0	42	79	99	135
10°C, 0°/oo	:				
mean l	: 0.96	1.45	1.76	1.96	2.19
s.d.	: 0.19	0.32	0.26	0.34	0.32
10°C, 7°/oo	:				
mean l	: 0.93	1.46	1.81	1.89	2.03
s.d.	: 0.19	0.34	0.43	0.45	0.46
10°C, 14°/oo	:				
mean l	: 0.93	1.59	1.89	1.91	1.94
s.d.	: 0.16	0.15	0.27	0.26	0.26

Time, days	0	42	79	99	135
10°C, 21°/oo					
mean l	0.91	1.20	1.45	1.55	1.58
s.d.	0.16	0.17	0.27	0.32	0.36
10°C, 28°/oo					
mean l	0.99	1.06	1.18	1.28	1.4
s.d.	0.15	0.18	0.21	0.17	0.19

Time, days	0	20	43	69	99	132
15°C, 0°/oo						
mean l	0.99	1.4	1.78	2.01	2.08	2.07
s.d.	0.21	0.25	0.23	0.31	0.34	0.33
15°C, 7°/oo						
mean l	0.98	1.59	2.13	2.29	2.4	2.45
s.d.	0.13	0.19	0.28	0.30	0.36	0.40
15°C, 14°/oo						
mean l	0.93	1.36	1.88	1.99	2.0	2.05
s.d.	0.16	0.23	0.24	0.23	0.24	0.21
15°C, 21°/oo						
mean l	0.95	1.12	1.44	1.65	1.7	1.73
s.d.	0.18	0.25	0.29	0.33	0.36	0.42
15°C, 28°/oo						
mean l	0.97	1.03	1.19	1.52	1.67	1.69
s.d.	0.17	0.21	0.34	0.35	0.35	0.37

Time, days	0	19	41	65	98	134
25°C, 0°/oo						
mean l	1.08	1.98	2.31	2.44	2.38	2.38
s.d.	0.27	0.33	0.47	0.5	0.42	0.45
25°C, 7°/oo						
mean l	0.95	2.28	2.54	2.61	2.63	2.64
s.d.	0.2	0.2	0.35	0.37	0.36	0.37
25°C, 14°/oo						
mean l	0.96	1.56	1.83	1.84	1.89	1.93
s.d.	0.13	0.50	0.44	0.43	0.43	0.37
25°C, 21°/oo						
mean l	1.03	1.8	1.93	1.94	1.96	1.97
s.d.	0.09	0.29	0.39	0.39	0.41	0.42

Time, days	0	15	38	56	89	126
25°C, 28°/oo						
mean l	0.97	1.09	1.41	1.50	1.52	1.53
s.d.	0.09	0.09	0.25	0.26	0.26	0.28

30°C, 0°/oo : no growth was acheived by these animals.
40% mortality after 13 days.
100% " " 35 ".

Time. days	0	13	35	59	104	162
30°C, 7°/oo						
mean l	0.92	1.12	1.45*	1.53	1.54	100% mortality
s.d.	0.16	0.24	0.41	0.40	0.39	*20% "

Time, days	:	0	13	35	59	104	162	
30°C, 14°/oo	:							
mean l	:	0.94	1.45	1.92	1.91	1.96	80%	mortality
s.d.	:	0.14	0.24	0.43	0.35	0.42	30%	"
30°C, 21°/oo	:							
mean l	:	1.0	1.18	1.35	1.41	1.41		
s.d.	:	0.15	0.24	0.30	0.33	0.32		
Time, days	:	0	15	30	56	105		
30°C, 28°/oo	:							
mean l	:	0.94	1.0	1.08	1.15	1.16		
s.d.	:	0.12	0.11	0.13	0.05	0.0		

Table 11

Results of growth experiment 2b. This shows the effect of cold exposure on the growth of 'summer' P. jenkinsi. The animals used are the 15°C grown P. jenkinsi from expt. 2a. After 132 days of growth in this expt.(2a) they were transferred to 5°C until day 167. They were then returned to 15°C until day 200 when they were measured. The mean lengths and standard deviations of sets of animals growing at different salinities are presented.

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als growing

Time, days	:	132 - 167 (5°C),	167 - 200 (15°C), 200
0°/oo	:		
mean l	:	2.07	2.13
s.d	:	0.33	0.32
7°/oo	:		
mean l	:	2.45	2.53
s.d.	:	0.40	0.39
14°/oo	:		
mean l	:	2.05	2.09
s.d.	:	0.21	0.22
21°/oo	:		
mean l	:	1.73	1.74
s.d.	:	0.42	0.42
28°/oo	:		
mean l	:	1.69	1.71
s.d.	:	0.37	0.39

Growth experiment (3) The growth of the P. jenkinsi used in this experiment was generally vigorous. The effects of salinity and temperature on growth are clearly defined. These animals, collected in December 1974, appear to show a bigger growth potential than those collected in July 1974 and used in experiment (2a). The results of experiment (1) started in January 1974 are comparable to these for animals collected in December 1974 (Tables 9 and 12 respectively).

As a result of the general vigour of the animals and the clear differential results for salinity and temperature variation, the analysis of the effects of these 'environmental' factors is based on experiment (3) (see Fig 12).

Growth experiment (4) All of the animals used in this experiment were collected in April 1975. Those which were grown in freshly collected water grew less quickly than animals in comparable conditio in experiment (3) started in December. The July animals in experiment (2a) grew very slowly. Further, in experiment (3) the animals growing in 3.5°/oo water, which were collected in January, a month after the others, exhibited growth rates faster than those predicted by Fig 12 based on the December animals. Thus if it can be assumed that the water and food quality were reasonably constant, there is a definite seasonal variation in growth potential such that the growth of winter animals is greater (potentially) than that of spring animals which in turn grow faster than those collected in the summer (Tables 10,12 and 13).

The assumption about water and food quality is tested in this experiment (Table 14). The results are not conclusive possibly due to the use of small numbers of animals. Analysis of variance was employed both before and after growth in the different waters (from experiment 2a - July, experiment 3 -December, and freshly made up water). Before treatment the F ratio (0.2910, d.f. - 5,23) was

Table 12

Results of growth experiment 3. The mean lengths and standard deviations of sets of ten animals, each set growing under different conditions of salinity and temperature, are shown. The times of the measurements, in days, are presented.

an lengths

each set

nd temperature,

s, are presented.

Time, days	0	15	57	126	157
5°C, 0°/oo					
mean l	1.36	1.38	1.38	1.66	1.74
s.d.	0.17	0.17	0.17	0.24	0.27
5°C, 7°/oo					
mean l	1.07	1.11	1.11	1.45	1.64
s.d.	0.10	0.10	0.10	0.28	0.28
5°C, 14°/oo					
mean l	1.28	1.28	1.31	1.82	1.97
s.d.	0.17	0.20	0.20	0.26	0.30
5°C, 21°/oo					
mean l	1.21	1.22	1.25	1.62	1.67
s.d.	0.1	0.14	0.14	0.17	0.20
5°C, 28°/oo					
mean l	1.18	1.23	1.23	1.35	
s.d.	0.22	0.20	0.20	0.33	

Time, days	0	15	36	56	71	93	126	167
10°C, 0°/oo								
mean l	1.15	1.26	1.60	2.04	2.33	2.74	3.32	3.54
s.d.	0.10	0.14	0.17	0.31	0.35	0.45	0.52	0.52
10°C, 7°/oo								
mean l	1.13	1.26	1.67	2.19	2.68	3.46	4.04	4.23
s.d.	0.14	0.17	0.30	0.38	0.36	0.28	0.20	0.24
10°C, 14°/oo								
mean l	1.13	1.34	1.87	2.46	2.98	3.45	3.97	4.06
s.d.	0.20	0.20	0.28	0.45	0.48	0.36	0.32	0.35

Time, days	0	15	36	56	71	93	126	167
10°C, 21°/oo								
mean l	1.07	1.20	1.50	1.90	2.29	2.83	3.47	3.65
s.d.	0.10	0.14	0.17	0.26	0.33	0.41	0.45	0.52
10°C, 28°/oo								
mean l	1.15	1.18	1.33	1.48	1.67	2.04	2.18	2.37
s.d.	0.14	0.14	0.20	0.30	0.36	0.42	0.47	0.49

Time, days	0	15	35	55	70	84	111
15°C, 0°/oo							
mean l	1.16	1.39	1.82	2.25	2.65	3.0	3.47
s.d.	0.14	0.14	0.42	0.66	0.77	0.79	0.74
15°C, 7°/oo							
mean l	1.22	1.46	2.35	3.27	3.92	4.27	4.43
s.d.	0.14	0.14	0.20	0.41	0.52	0.49	0.40
15°C, 14°/oo							
mean l	1.22	1.46	2.35	3.27	3.92	4.27	4.43
s.d.	0.14	0.14	0.20	0.41	0.52	0.49	0.40
15°C, 21°/oo							
mean l	1.19	1.39	2.17	2.97	3.55	4.0	4.24
s.d.	0.17	0.17	0.26	0.14	0.36	0.41	0.39
15°C, 28°/oo							
mean l	1.26	1.33	1.82	2.25	2.62	2.90	3.20
s.d.	0.14	0.17	0.46	0.40	0.42	0.48	0.41

Time, days	0	15	36	49	71	85	121
25°C, 0°/oo							
mean l	1.22	1.83	2.67	3.23	3.73	3.92	3.96
s.d.	0.20	0.44	0.99	0.81	0.66	0.64	0.60
25°C, 7°/oo							
mean l	1.26	2.48	4.75	5.02	5.08		
s.d.	0.14	0.24	0.41	0.32	0.22		
25°C, 14°/oo							
mean l	1.25	2.67	4.92	4.99	5.03		
s.d.	0.14	0.24	0.26	0.22	0.24		
25°C, 21°/oo							
mean l	1.12	2.06	4.38	4.89	5.04		
s.d.	0.10	0.28	0.33	0.50	0.60		
25°C, 28°/oo							
mean l	1.11	1.31	2.36	2.86	3.52		
s.d.	0.10	0.20	0.67	0.77	1.03		

Time, days	0	15	36	56	71	85
30°C, 0°/oo						
mean l	1.3	1.43	2.16	2.53	2.72	2.76
s.d.	0.22	0.22	0.63	0.57	0.57	0.58
30°C, 7°/oo						
mean l	1.18	2.03	3.96	4.03	4.1	
s.d.	0.17	0.41	0.53	0.55	0.57	
30°C, 14°/oo						
mean l	1.21	2.35	3.88	4.08	4.14	
s.d.	0.14	0.14	0.57	0.53	0.57	

Time, days	:	0	15	36	56	71	85
30°C, 21°/oo	:						
mean l	:	1.12	1.73	3.25	3.42	3.46	
s.d.	:	0.17	0.35	0.47	0.54	0.55	
30°C, 28°/oo	:						
mean l	:	1.2	1.3	2.13	2.36	2.40	2.40
s.d.	:	0.17	0.22	0.42	0.35	0.35	0.35

Table 13

Results of growth experiment 4. All the animals were grown at 25°C. They were grown in July expt. water (expt. 2a), freshly mixed (April) water and december expt. water (expt.3). In each group water of 7 and 14°/oo was used.

The mean lengths and standard deviations are shown. The times of the measuements, in days, are presented.

Time, days	0	15	52	86
July experimental water				
7°/oo, n=4				
mean l	1.43	2.36	3.59	4.10
s.d.	0.0	0.14	0.69	0.56
July experimental water				
14°/oo, n=4				
mean l	1.38	1.73	3.25	3.31
s.d.	0.1	0.2	0.3	0.2
Freshly made (April) water				
7°/oo, n=6				
mean l	1.48	2.45	4.06	4.19
s.d.	0.17	0.32	0.42	0.41
Freshly made (April) water				
14°/oo, n=6				
mean l	1.41	2.22	3.95	4.07
s.d.	0.14	0.20	0.39	0.45
Dec. experimental water				
7°/oo, n=5				
mean l	1.42	1.86	2.98	3.20
s.d.	0.14	0.20	0.65	0.82
Dec. experimental water				
14°/oo, n=5				
mean l	1.44	2.29	3.70	3.86
s.d.	0.14	0.24	0.37	0.35

e animals
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nted.

Table 14

Statistics for growth experiment 4. See pages 20 - 23. The results of t tests and analyses of variance.

e pages 20 -

nce.

Analysis of variance :

between all temp. - sal. sets pre - growth : not sig. 95% (F)

" " " " " post - growth : sig. 95% (F)

Students t test

April vs. July & Dec. pooled - $14^{o}/oo$, t - sig. 90%, F not sig. 90%

" " " " " " - $7^{o}/oo$, t - sig. 90%, F not sig. 90%

April vs. July - $14^{o}/oo$, t sig. 98%, F not sig. 90%

" " " - $7^{o}/oo$, t not sig. 90%, F " " "

" " Dec. - $14^{o}/oo$, t not sig. 90%, F " " "

" " " - $7^{o}/oo$, t sig. 95%, F " " "

July vs. Dec. - $14^{o}/oo$, t sig. 95%, F not sig. 90%

" " " - $7^{o}/oo$, t not sig. 90%, F " " "

insignificant. After growth the F ratio (3.5383, d.f. -5,23) was significant at 95 % (Table 14). Thus the treatment (growth in different water and with different food) caused a difference in growth. This was analysed further, using t tests. Pooling the results from the animals grown in July and December experimental water, they are significantly different to those for animals grown in freshly made up water. Thus it appears that growth is significantly (at the 90% level) depressed in the previously used water as opposed to freshly made salinities. However, individual comparisons of the effects of freshly made salinities (and food) as compared to previously used materials show variable results (Table 14).

The causes of reduced growth in the water from the July and December experiments may be either (1) conditioning of the media by the previous occupants (should be similar in both cases) or (2) some inadequacy or contaminant in the food or water having adverse effects on the animals.

Distinguishing between these alternatives is difficult since the results are not conclusive. However, since the December experimental food and water did support rapid growth in experiment (3) whilst the July food and water supported only poor growth in experiment (2a), some interpretation is possible. Slow growth in the December food and water in experiment (4) must be due to the conditioning of the media by the previous occupants since the latter grew well, confirming the absence of any unfavouable factors. Growth in the December 7°/oo water was significantly reduced in relation to the growth in the freshly made up control. Growth suppression was not observed in the December 14°/oo water. In addition to conditioning of the media slow growth in the July

water could be due to adverse food or water conditions, present when these materials were collected. This could explain the slow growth in experiment (2a). However, the July media did not give consistently slower growth than the December food and water. Those animals in 7°/oo saline water grew at the same rate. Thus it has been shown that the 7°/oo media used in the July growth experiment (2a) was capable of supporting growth at similar rates to those supported by the water from experiment (3) (December).

The growth of the animals in the July 14 °/oo water is significantly suppressed as compared to that of the P. jenkinsi in December 14°/oo water. Two explanations seem consistent with the fact that the July 14°/oo water suppressed growth whilst the July 7°/oo water did not : (1) There was a contaminant in the sea water and thus higher salinities caused more suppression or (2) there was a contaminant either in the fresh water, the sea water or the food leaves which interacted with a component of the saline water,such that the higher the salinity the more adverse the effect. Hypothesis (2) may be considered consistent with the results of experiment (2a) in which the growth of P. jenkinsi in fresh water, ,whilst suppressed in relation to growth under similar conditions in experiment (3), equals or exceeds the growth of animals in 7, 14 and 21°/oo salinity. In experiment (3), where growth was generally more vigorous, these saline waters supported faster growth to larger final sizes (Figs 12 and 13, Table 12) Hypothesis (1) is unlikely since growth in fresh water was suppressed.

Thus there is no conclusive evidence for or against the hypothesis that the poor growth observed in experiment (2a) was due to factors associated with the food or water. However, both the 7°/oo and 14°/oo

saline water from experiment (2a) did support more rapid growth to larger final sizes using the animals taken in April than in the origi nal experiment using animals collected in July. There is a possibility that favourable conditioning of the media by the previous occupants would explain this. However, this is unlikely since the opposite was observed using the December water. It is believed that overall, the evidence favours the possibility that there were endogenous differences in the animals taken and used in experiments started at different times of the year and that this variation caused the disparate growth performance observed.

Growth, Salinity and Temperature. The results of growth experiment (3) are those on which the discussion of the effects of salinity and temperature is based. The other experiments were either too limited in extent (1, 2b and 4) or subject to some suppression of growth (2a). Since the animals in experiment (3) show a generally rapid rate of growth,the discussion of the relative effects of salinity and temperature must take account of the general favourability of the environment and condition of the animals.Under such favourable conditions, considerable temperature and salinity dependent variation in growth was observed. In generally less favourable conditions or with animals having a low potential for growth such environmentally induced differences are comparatively small. Table 10 shows the generally suppressed and relatively uniform growth found in experiment (2a), started in July, as opposed to the comparatively vigorous growth shown by the animals in experiment (3) begun in December (Table 12). This variation in

the growth of P. jenkinsi with salinity and temperature (experiment 3) is shown in Figs 6 - 12.

It may be postulated that under favourable conditions and with animals capable of exploiting them there is'more room' for the expression of variation due to particular environmental parameters. Under generally sub - optimal conditions or with animals intrinsically incapable of rapid growth the maximum and minimum growth rates are close together and the effects of modifying variables are likely to be reduced. The results of this work support this view.

Both the two dimensional graphs of log length vs. time (Figs 6 -11) and the three dimensional graph (Fig 12) show the variation of the growth rate of P. jenkinsi with the environmental variables temperature and salinity. The form of the growth curves (length vs. time) would be sigmoid on a linear scaled plot but the use of log l in Figs 6 - 11 linearises the initial exponential part of the curve. The lines were fitted by eye and the slopes of these were divided by 2.303 to give growth rate k values (to the base e)(Calow 1973). These values (k_e^1) were employed in Fig 12. This graph clearly shows that the optimal conditions for the growth of P. jenkinsi are 25°C and 14°/oo salinity. At all temperatures 14°/oo salinity is optimal and at all salinities 25°C maximises the growth rate.

The growth rates are shown in Table 15. This includes those for animals grown in water at 3.5°/oo salinity. These were obtained using animals collectedat a different time and thus give results which are not strictly comparable to the others in the table. These results are plotted in Fig 11. They too show a peak of growth activity at 25°C. The difference between these results and what might have been predicted from Fig 12 may be a reflection of the seasonal variation

Figure 6

Graphs of the growth of P. jenkinsi at 5°C. Each line represents growth at a different salinity. Log length is plotted against time in days.

5°C - 0°/oo - •

5°C - 7°/oo - ▪

5°C - 14°/oo - ▫

5°C - 21°/oo - ◦

5°C - 28°/oo - ◆

t 5°C. Each

Log length

Figure 7

Graphs of the growth of P. jenkinsi at 10°C. Each line represents growth at a different salinity. Log length is plotted against time in days.

10°C - 0°/oo - •

10°C - 7°/oo - ▪

10°C - 14°/oo - ▫

10°C - 21°/oo - ○

10°C - 28°/oo - ◆

t 10°C. Each

. Log length

Figure 8

Graphs of the growth of P. jenkinsi at 15°C. Each line represents growth at a different salinity. Log length is plotted against time in days.

15°C - 0°/oo - •

15°C - 7°/oo - ▪

15°C - 14°/oo - ▫

15°C - 21°/oo - ○

15°C - 28°/oo - ♦

t 15°C. Each

Log length

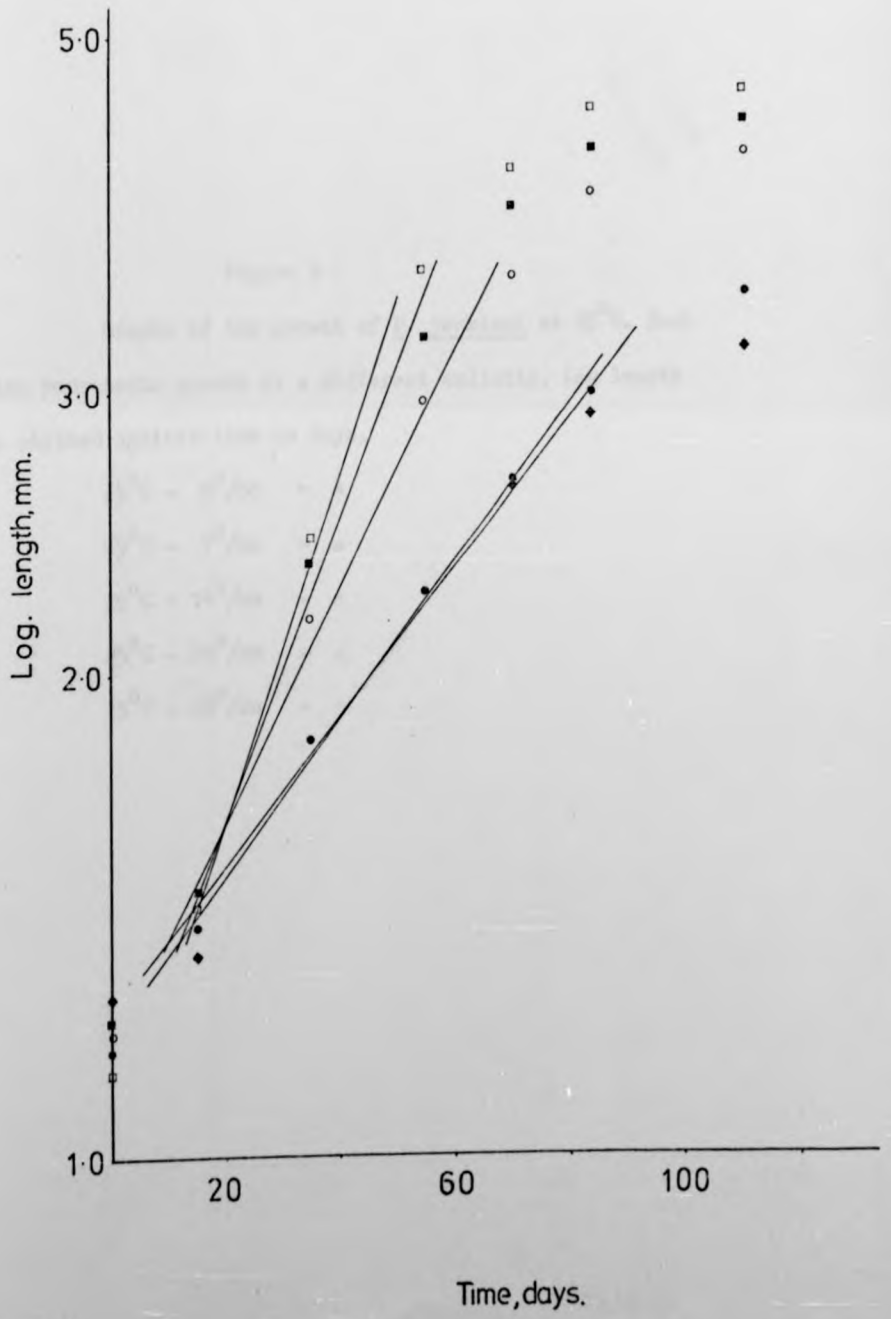


Figure 9

Graphs of the growth of P. jenkinsi at 25°C. Each line represents growth at a different salinity. Log length is plotted against time in days.

25°C - 0°/oo - •

25°C - 7°/oo - ▪

25°C - 14°/oo - ▫

25°C - 21°/oo - ◦

25°C - 28°/oo - ◇

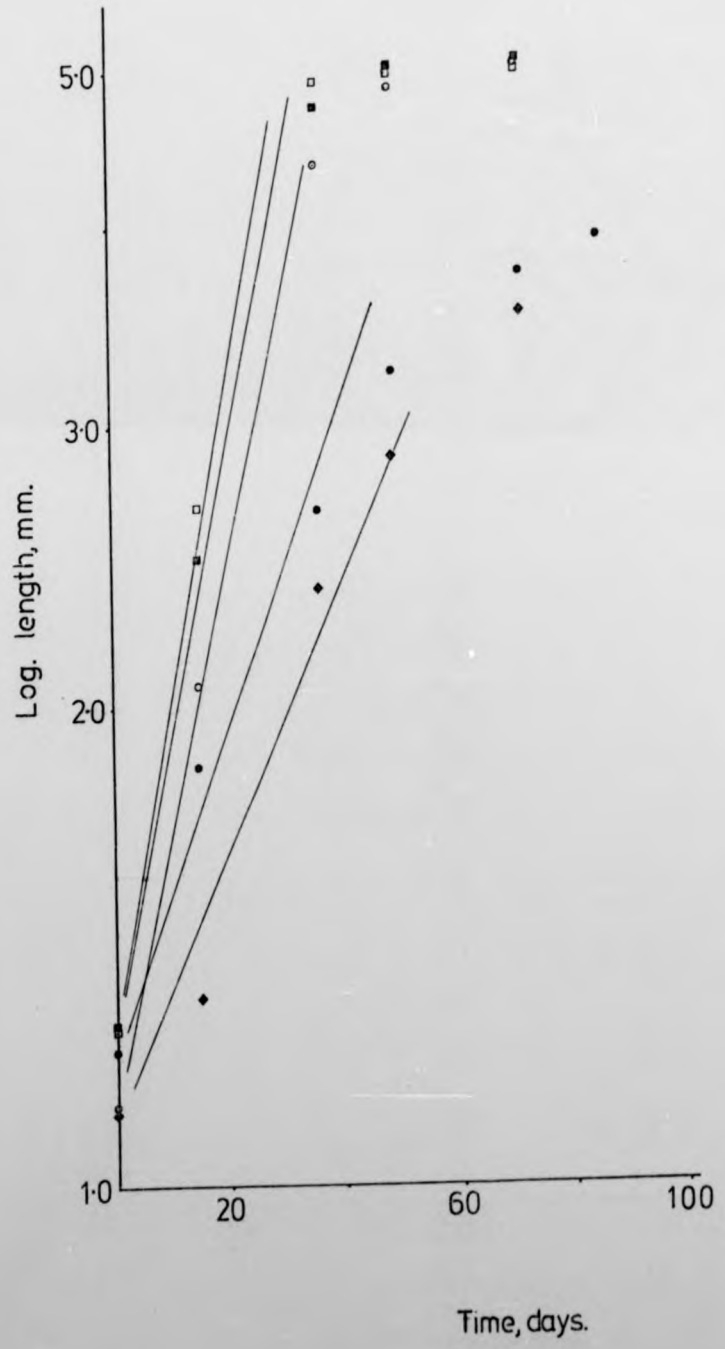

5·0
3·0
2·0
1·0
Log. length, mm.
20
60
100
Time, days.

Figure 10

Graphs of the growth of P. jenkinsi at 30°C. Each line represents growth at a different salinity. Log length is plotted against time in days.

30°C - 0°/oo - •

30°C - 7°/oo - ▪

30°C - 14°/oo - ▫

30°C - 21°/oo - ◦

30°C - 28°/oo - ◆

at 30°C. Each

y. Log length

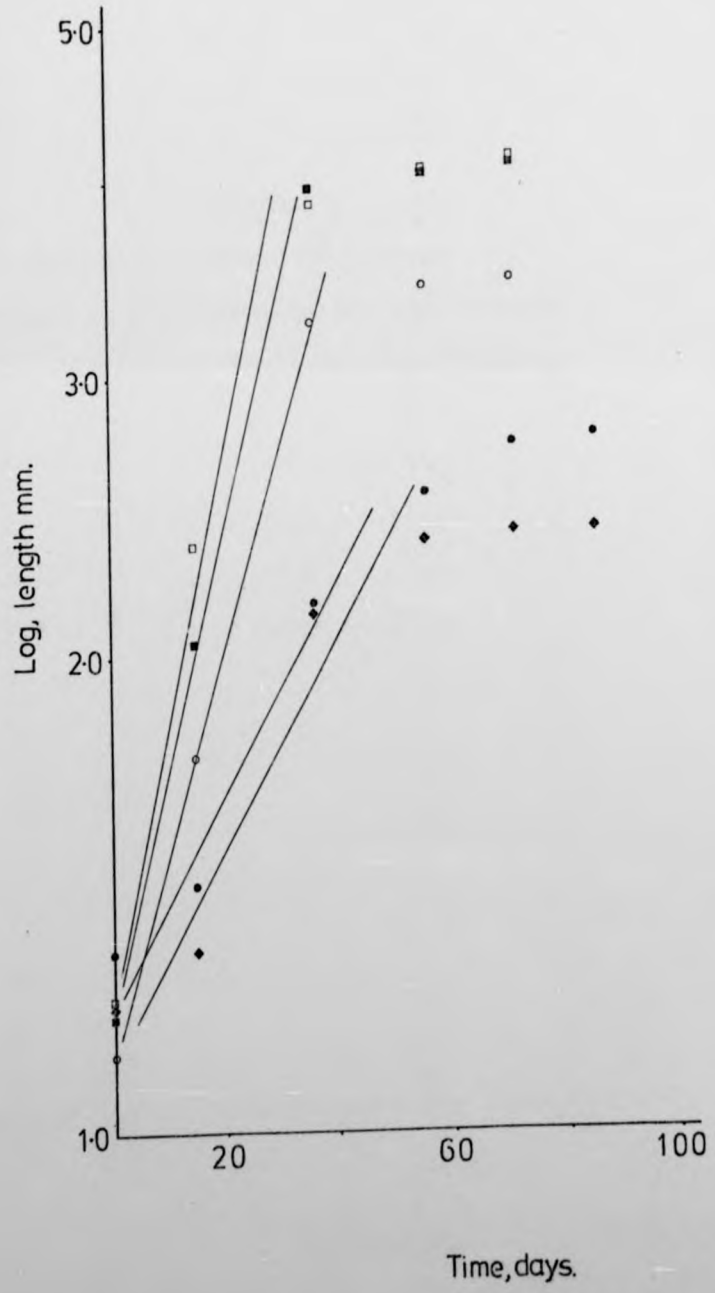


Figure 11

Graphs of the growth of P. jenkinsi at 3.5°/oo salinity. Each line represents growth at a different temperature. Log length is plotted against time in days.

3.5°/oo - 10°C - •

3.5°/oo - 15°C - ▪

3.5°/oo - 25°C - ▫

3.5°/oo - 30°C - ○

at 3.5°/oo

fferent temperature.

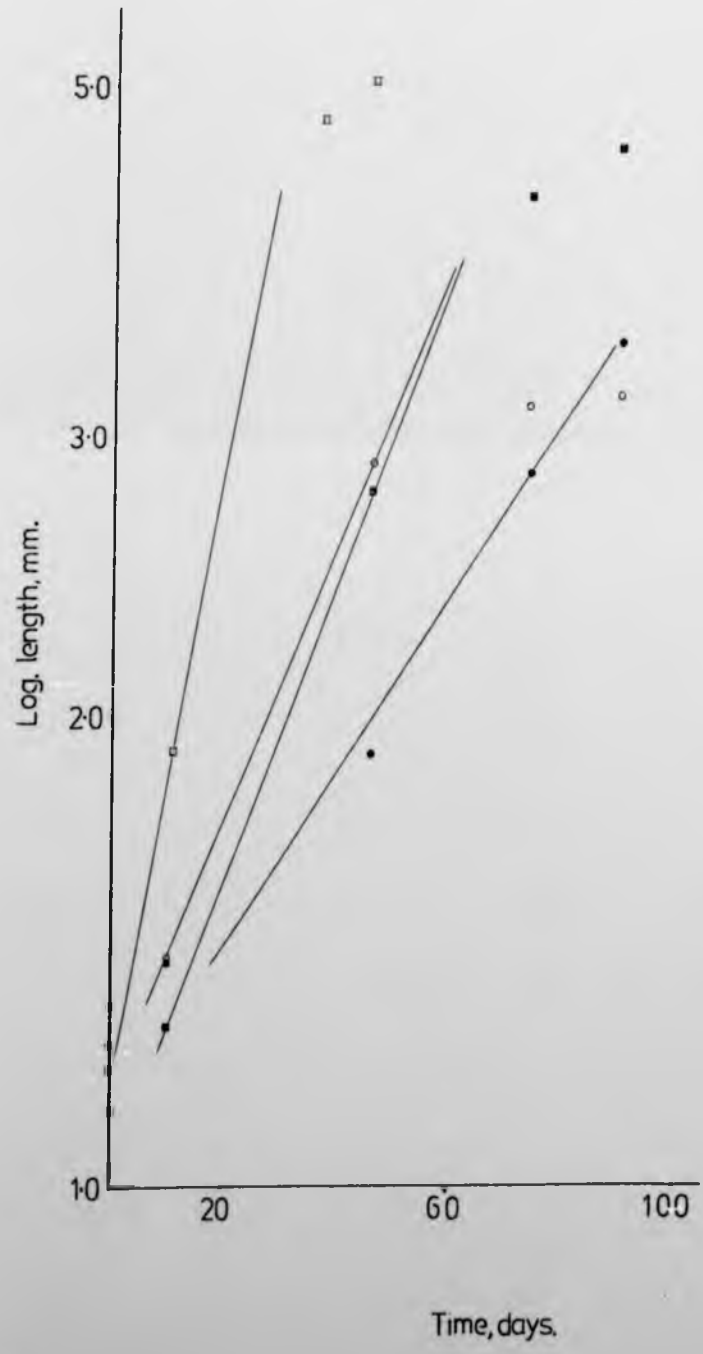


Table 15

Growth rate k values based on shell length (k_e^1). The values of k_e^1 are presented in a temperature - salinity matrix. (see pages 24 and 25)

length (k_e^1).

re - salinity

Salinity°/oo.	Temperature°C : 5	10	15	25	30
0	0.0005	0.0022	0.0021	0.0045	0.0030
7	0.0007	0.0025	0.0040	0.0081	0.0066
14	0.0009	0.0026	0.0047	0.0087	0.0075
21	0.0007	0.0022	0.0032	0.0075	0.0056
28	0.0003	0.0014	0.0020	0.0036	0.0030
• 3.5		0.0024	0.0041	0.0085	0.0037

Figure 12

A three dimensional graph of growth rate k (based on shell length, k_e^1) vs. salinity ($^o/oo$) and temperature (^oC). The most rapid growth occurs at 25^oC and $14^o/oo$.

rate k (based

temperature (°C).

‰.

in growth potential discussed previously.

The results shown in Table 15 : the exponential growth rate values, based on shell length (k_e^l), were converted to carbon based values using the allometric regression relations of log length vs. log organic carbon (Fig 3 and Table 1 - section 2.3.). The k values in carbon terms are presented in Table 16 and Fig 13a, which is similar to the linearly based version (Fig 12). The carbon based growth rates are referred to as : k_e^c .

Since the growth rate values in both length and carbon terms are vital to this work their calculation will be explained in detail. The relation between log l and time is linear (initially) (Figs 6 - 11). The k_e^l values were calculated from Figs 6 - 11 :

$$k_e^l = \frac{\log l_2 - \log l_1}{t_2 - t_1} \times \frac{1}{2.303}$$

Using the relationships : log c = m log l + a (Table 1) the terms log c_2 and log c_1 could be substituted in place of log l_2 and log l_1 respectively :

$$K_e^c = \frac{\log c_2 - \log c_1}{t_2 - t_1} \times \frac{1}{2.303}$$

l = shell length, c = organic carbon, t = time
(mm) (ug) (days)

1/2.303 converts k_{10} to k_e .

The calculation of k_e^c is based on the assumption that log c is linearly related to time (initially). This has been confirmed and Fig 13b is

Table 16

Growth rate k values based on organic carbon (k_e^c). The values of k_e^c are presented in a temperature - salinity matrix. (see pages 24 and 25)

nic carbon (k_e^c).

ure - salinity

Salinity °/oo.	Temperature °C : 5	10	15	25	30
0	0.0015	0.0055	0.0050	0.0108	0.0059
7	0.0020	0.0062	0.0086	0.0191	0.0167
14	0.0025	0.0065	0.0109	0.0208	0.0169
21	0.0014	0.0052	0.0076	0.0184	0.0132
28	0.0005	0.0027	0.0039	0.0085*	0.0068*

Figure 13a

A three dimensional graph of growth rate k (based on organic carbon, k_e^c) vs. salinity ($^o/oo$) and temperature (^oC). As in Fig 12 where k_e^l was plotted the most rapid growth occurs at 25^oC and $14^o/oo$.

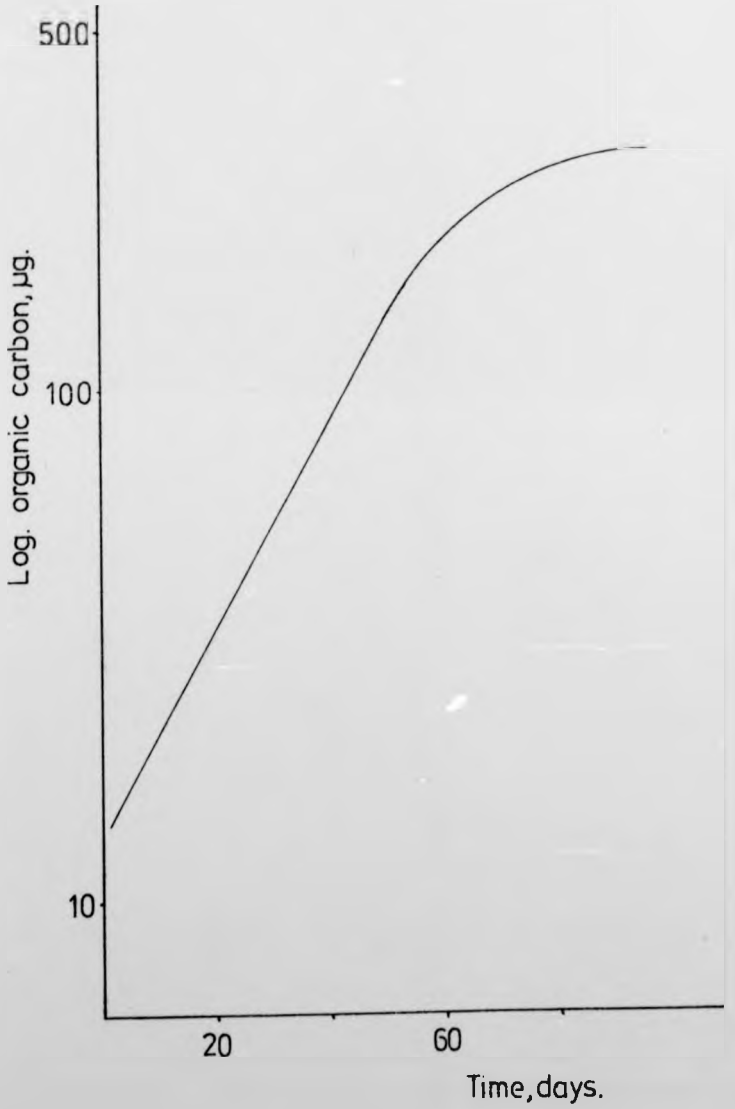
h rate k (based
and temperature (°C).
apid growth occurs

Figure 13b

An example of a plot of log organic carbon vs. time. This graph emloys data from animals grown at $7^{o}/oo$ and $15^{o}C$.

The numbers on the log carbon axis are 'unlogged' carbon values (μg.)

The log carbon axis is in $\log_{10}$. The slope (carbon growth rate) is k^{c}_{10}. This was divided by 2.303 to give the k^{c}_{e} value. These (for all combinations of salinity and temperature) are presented in Table 16 and Fig 13a. (see page 25)



c carbon vs.

own at 7°/oo

are 'unlogged'

he slope (carbon

03 to give the

inity and temperature)

page 25)

an example of such a relationship, in this case for animals grown at $7^{o}/oo$ salinity and $15^{o}C$. Comparing this curve to Figs 6 - 11 shows the similar growth form exhibited by length and organic carbon in this species. The relations between growth in time, based on length, weight and organic carbon, will vary with the geometry and chemical composition of the species. Molluscs such as P. jenkinsi which grow in a spiral pattern and which have large heavy shells, consisting largely of $CaCO_3$ will presumably show some differences to other species lacking these features.

Synergistic interaction. Fig 14 shows the effect of the synergistic interaction between temperature and salinity on the growth rate of P. jenkinsi. This should be related to Table 16 from which the values are calculated. The presence and degree of synergistic interaction was determined as follows :

		Temperature	
		1	2
Salinity	1	a	b
		s	
	2	c	d

a, b, c and d are experimental growth rates (carbon) and in this case d is greater than b and c, which are both greater than a. (temperature and salinity combination 2/2 is more favourable than 2/1 or 1/2 which are both more favourable than 1/1).

Thus in this work, the interactions are calculated 'towards' the more favourable conditions but s may be positive or negetive. s is the 'degree of synergistic interaction' and may be

Figure 14

This is a temperature - salinity matrix showing the 'degree of synergistic interaction'. The numbers presented are values of s (page 26). s denotes the degree of interaction between temperature and salinity in their effect on the growth of P. jenkinsi.

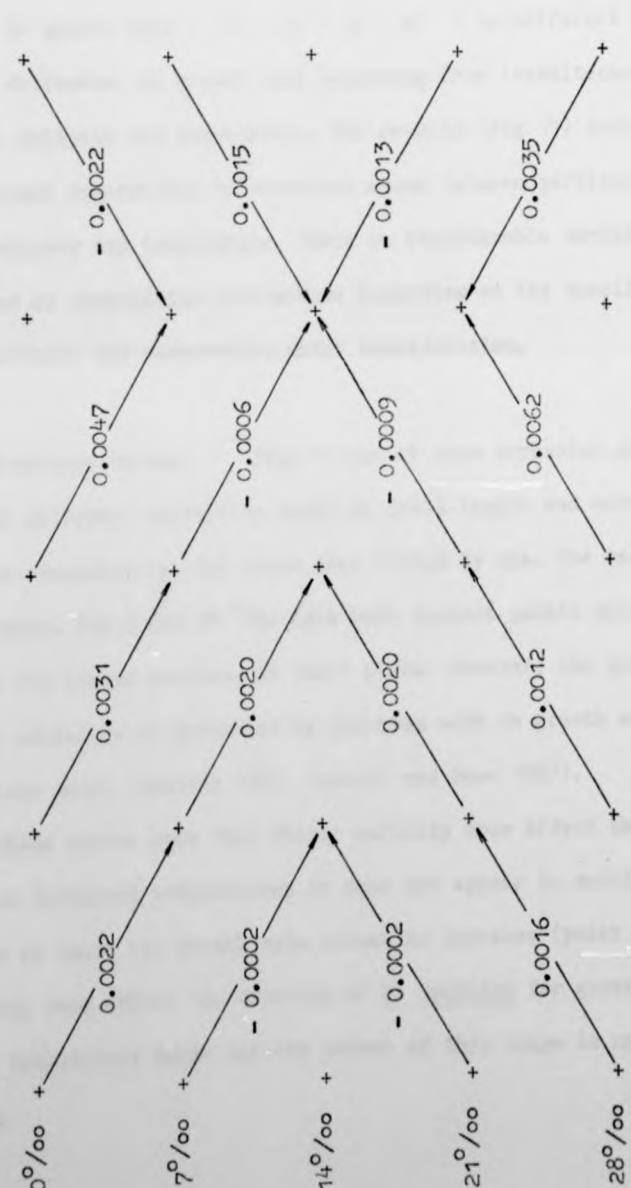
The + symbols correspond to the growth rates in table 16 - k_e^c .

s has only been calculated for a small number of the possible changes in the combination of salinity and temperature for growth. These are sufficient to show that synergism occurs and that the intensity of interaction varies with the particular combinations of salinity and temperature involved.

matrix showing
e numbers presented
egree of interaction
ffect on the growth

rowth rates in

small number of
salinity and
t to show that
interaction
salinity and



defined as follows :

$$s = (d - a) - (\ (b - a) + (c - a)\ )$$

Interactive effects are demonstrated when the sum of the separate differences in growth rate ((b - a) + (c - a)) is different to (d - a) the difference in growth rate resulting from 'simultaneous' variation in salinity and temperature. The results (Fig 14) indicate that significant synergistic interactions occur between particular levels of salinity and temperature. There is considerable variation in the degree of synergistic interaction depending on the specific levels of salinity and temperature under consideration.

Arrhenius Curves. Figs 15 and 16 show Arrhenius plots of growth at different salinities based on shell length and carbon growth rates respectively. The lines were fitted by eye. The results show some error. The 0 and 21 °/oo data both include points which depart from the linear sections of their plots. However, the general form of the curves is as predicted by previous work on growth employing the Arrhenious model (Brandts 1967, Farrell and Rose 1967).

These curves show that whilst salinity does affect the rate of growth at different temperatures it does not appear to modify the temperature at which the growth rate ceases to increase (point of inflection). Thus salinity does affect the capacity of P. jenkinsi for growth within its viable temperature range but the extent of this range is not influenced.

Figure 15

Arrhenius plots of growth rate. Each line represents growth at a different salinity. Growth rate (length - k_e^1) is plotted against $1/T^{\circ}A$.

$0^{\circ}/oo$ - •

$7^{\circ}/oo$ - ▪

$14^{\circ}/oo$ - ▫

$21^{\circ}/oo$ - ◦

$28^{\circ}/oo$ - •

h line represents

length - k_e^1) is

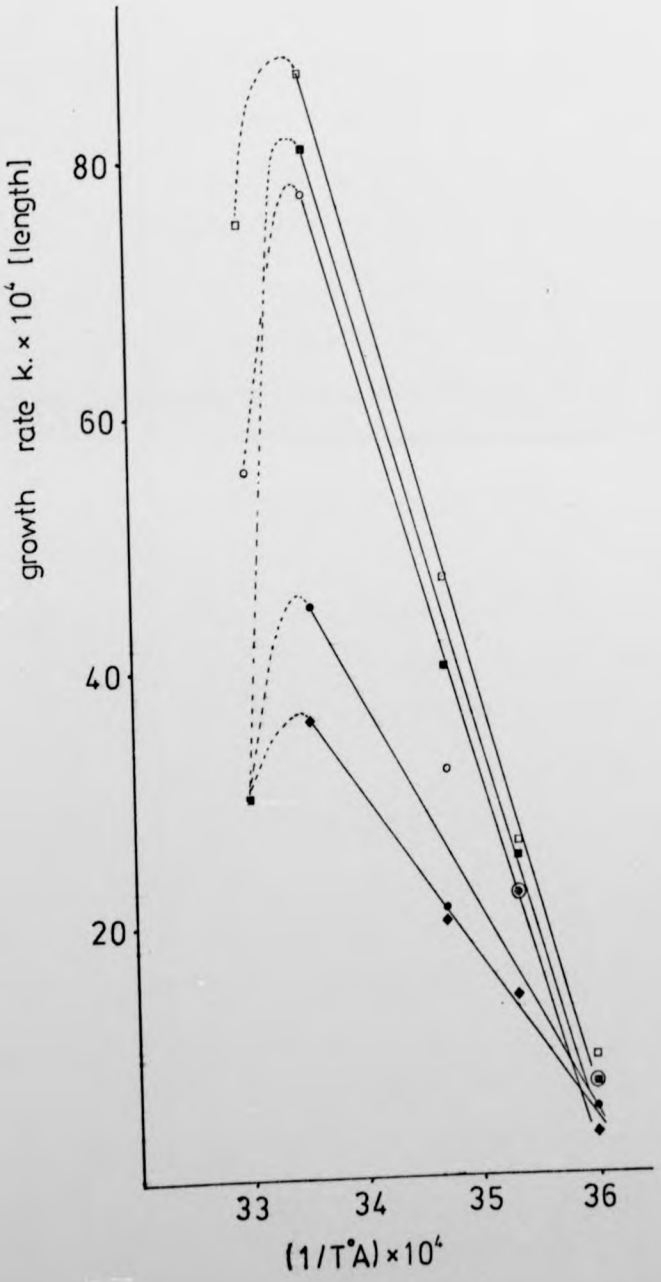


Figure 16

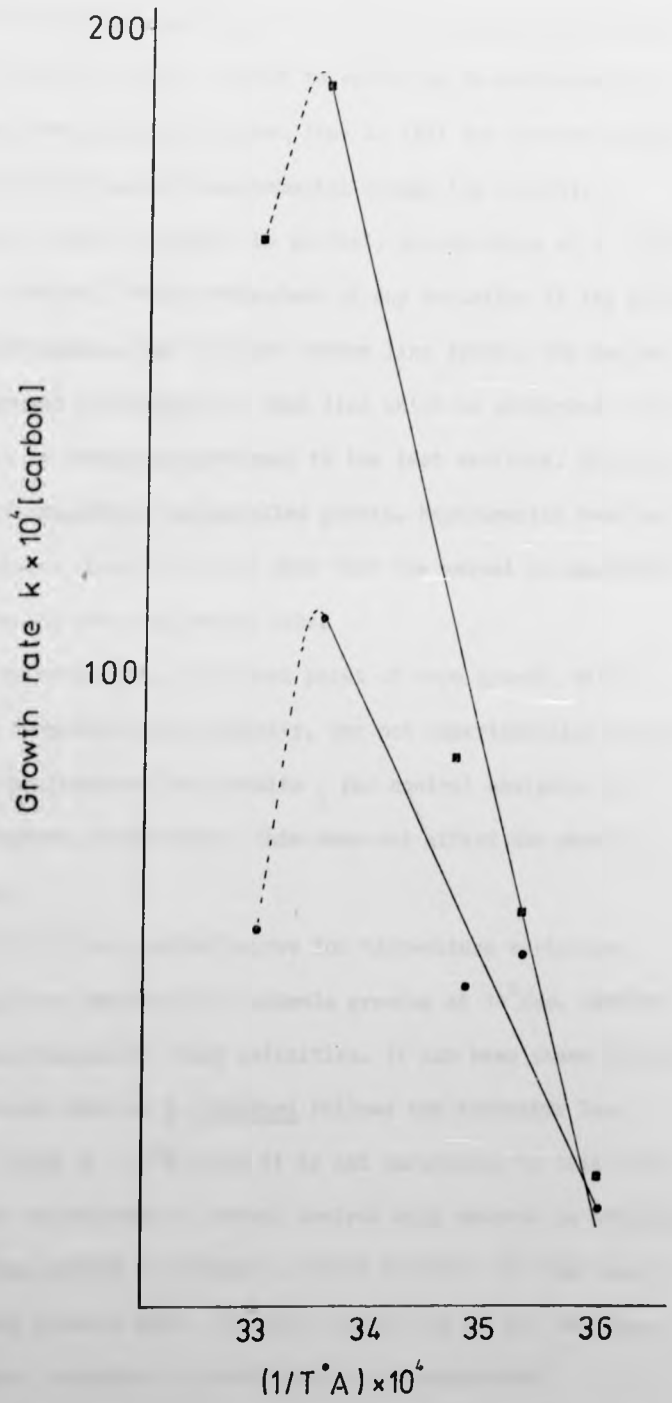
Arrhenius plots of growth rate. The lines represent growth at different salinities. Growth rate (organic carbon - k_e^c) is plotted against $1/T^{\circ}A$.

$0^{\circ}/oo$ - •

$7^{\circ}/oo$ - ▪

lines represent

organic carbon -



Growth Control. Control curves of the type used by Calow (1973) are shown in Figs 17 - 22. These demonstrate whether growth is controlled with respect to variation in environmental parameters. The horizontal broken line is that for perfect control of growth in the face of environmental change (in salinity or temperature). Thus if control is perfect, growth stays at a constant (maximum - optimal) rate independent of any variation in the factor under investigation. The straight broken line joining the maximum and zero growth coordinates is that line which is predicted if the growth rate is simply proportional to the test variable. This line is that for completely uncontrolled growth. Experimental results falling between these two lines show that the animal is exerting partial control over its growth rate.

Unfortunately, the exact point of zero growth, with respect to temperature and salinity, was not experimentally defined and so the precision of the results for control analysis, is reduced. However, as is shown, this does not affect the general conclusions.

Fig 17 is a control curve for temperature variation. This example was produced with animals growing at 14°/oo. Similar results are obtained at other salinities. It has been shown (Fig 16) that the growth rate of P. jenkinsi follows the Arrhenius law within the range 5 - 25°C. Thus it is not surprising to find that Fig 17 shows no evidence of growth control with respect to temperature variation. Zero growth is assumed to occur at about 3°C (the data approximately predict this). The line was fitted by eye and shows a proportional decrease in growth rate with temperature.

The results for salinity variation are different. At all

Figure 17

A graph showing that growth is not controlled with respect to temperature in P. jenkinsi. This is based on animals grown at 14°/oo salinity : similar graphs may be drawn using the growth data from the other salinities.

The horizontal pecked line is that for perfect control of growth (marked p.c.). The pecked line joining the maximum and zero growth coordinates is that for zero control (marked z.c.) The actual growth control line follows the latter showing that growth simply varies in proportion to temperature.

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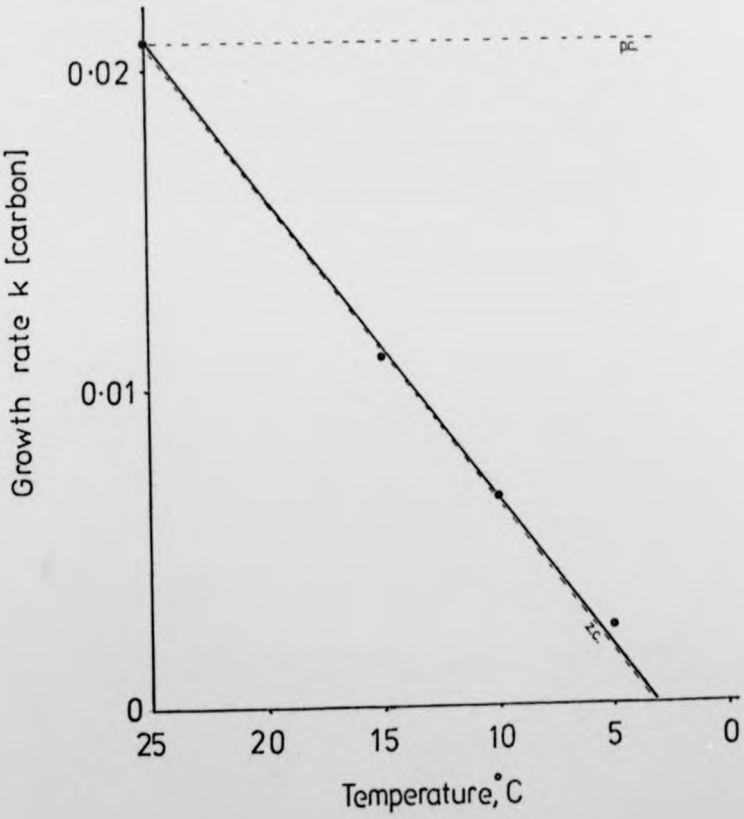

the temperatures used the snails were able to control their growth with respect to differences in salinity (Figs 18 - 22). In order to compare the results from different salinities, plots of the 'need for control' vs. the 'observed control' were produced (Figs 23 and 24). The 'need for control' is the difference in growth rate between perfect control and zero control whilst the 'observed control' is the difference between the experimental line and the zero control curve (Calow 1973). Abrupt breakdowns in control are demonstrated in Figs 23 and 24. On the salinity scale of Figs 18 - 22 fresh water is placed at a slightly higher salinity than 0°/oo at which growth is stated as zero. Because of the minute difference between the salinity of fresh water and that of the dilution for zero growth, in terms of the total salinity range of the experiments, errors in these graphs (and hence in Figs 23 - 25) due to the estimation of the 'position' of zero growth are negligible.

Fig 25 shows plots of the initial linear sections of the curves presented in Figs 23 and 24. The lines are fitted by eye. The results for 10 and 25°C conform to one 'higher' line whilst those for 5 and 15°C form another. There is no obvious explanation for this.

Figs 23 and 24 show that as the 'need for control' increases, in these cases with a fall in salinity from the optimum at 14°/oo to fresh water, the 'observed control' increases until a critical point is reached beyond which growth cannot be supported. This occurs at some dilution of the ionic content of fresh water.

P. jenkinsi also shows growth compensation at high salinities. However, it is impossible to estimate the high salinity point of zero growth with the available data and so the control curves cannot be drawn accurately.

Figures 18 and 19

Control curves for salinity at 5 and 10 °C respectively. Unlike temperature growth is controlled with respect to salinity. The growth rates (k_e^c) fall between the perfect and zero control lines (p.c. and z.c. - Fig 18 - respectively). At different temperatures the control of growth with respect to salinity follows a different pattern - Figs 18 - 22.

Figures 18 and 19

Control curves for salinity at 5 and 10 ^{o}C respectively. Unlike temperature growth is controlled with respect to salinity. The growth rates (k_e^c) fall between the perfect and zero control lines (p.c. and z.c. - Fig 18 - respectively). At different temperatures the control of growth with respect to salinity follows a different pattern - Figs 18 - 22.

10 °C

rolled

fall

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peratures

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Fig 18.

Fig 19.

Figures 20 and 21

Control curves for salinity at 15 and 25°C respectively. An intermediate level of control is observed (between perfect and zero).

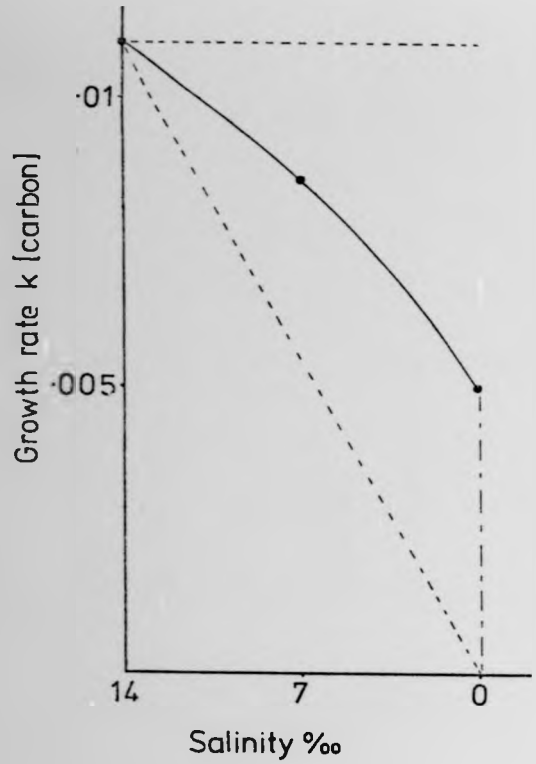
Growth rate k (carbon)
·01
·005
14
7
0
Salinity ‰

Fig 20.

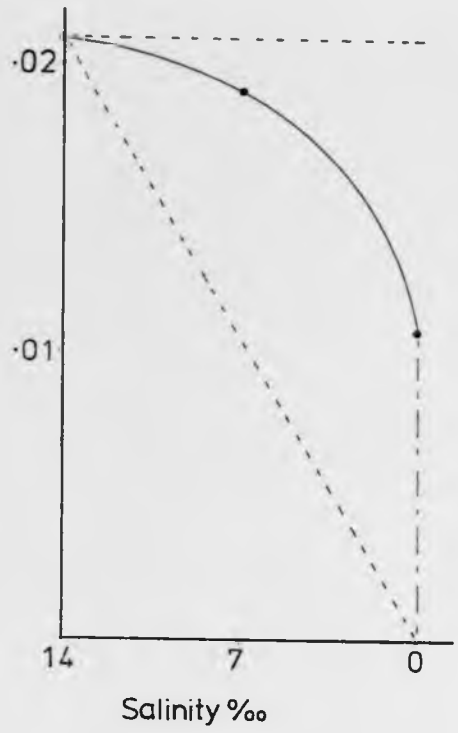
·02
·01
14
7
0
Salinity ‰

Fig 21.

Figure 22

A control curve for salinity at 30°C.

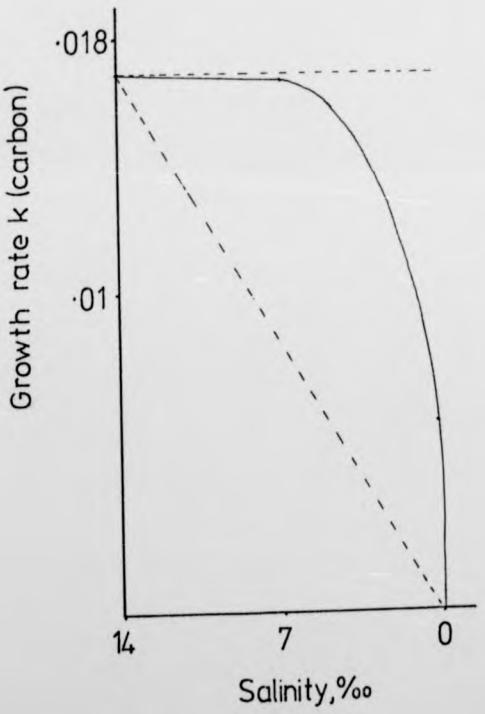
·018
·01
Growth rate k (carbon)
14
7
0
Salinity,‰

Table 17

The corresponding values of the 'need for control' and the 'observed control' for growth rate vs. salinity. These values are derived from Figs 18 - 21.

The 'need for control' is the difference in growth rate between perfect control and zero control (at specific salinities) whilst the'observed control' is the difference between the experimental line and the zero control curve (at corresponding salinities). (see page 29)

d for control'

salinity.

ence in growth

lat specific

difference

trol curve

25°C		15°C	
need	observed	need	observed
0.0000	0.0000	0.0000	0.0000
0.0024	0.0019	0.0012	0.0008
0.0040	0.0036	0.0021	0.0013
0.0058	0.0051	0.0031	0.0019
0.0077	0.0066	0.0041	0.0024
0.0096	0.0081	0.0050	0.0029
0.0133	0.0105	0.0070	0.0038
0.0152	0.0114	0.0089	0.0044
0.0171	0.0121	0.0099	0.0047
0.0190	0.0123	0.0103	0.0048
0.0200	0.0116	0.0109	0.0000
0.0208	0.0000		

10°C		5°C	
need	observed	need	observed
0.0000	0.0000	0.0000	0.0000
0.0007	0.00065	0.00025	0.00015
0.0018	0.00165	0.0007	0.0040
0.0030	0.00275	0.0016	0.0095
0.0042	0.00375	0.00205	0.00122
0.0053	0.0046	0.0024	0.00142
0.0064	0.00535	0.0025	0.0000
0.0065	0.0000		

Figure 23

Graphs of the 'need for control' vs. the 'observed control' of growth with respect to salinity. The two curves are for different temperatures :

$5^{o}C$ - ▪

$10^{o}C$ - •

These curves are derived from Figs 18 and 19 respectively. (see page 29 and Table 17)

the 'observed

e two curves

8 and 19 respectively.

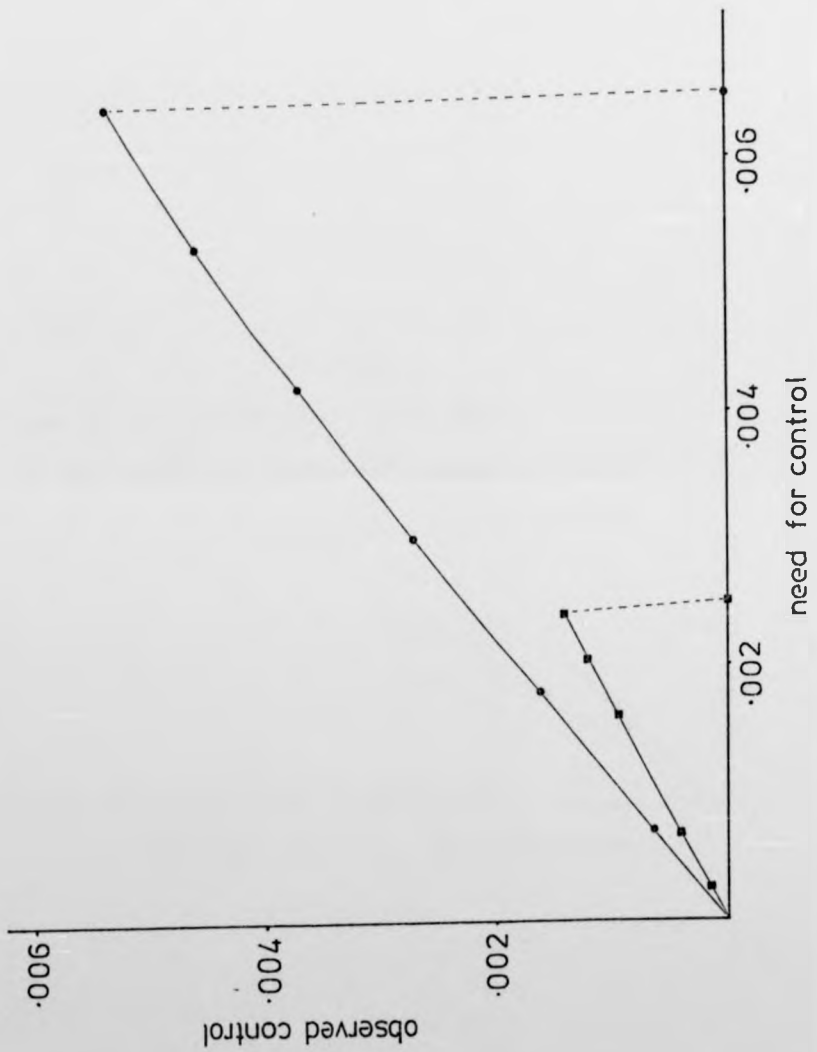

Figure 24

Graphs of the 'need for control' vs. the'observed control' of growth with respect to salinity. The two curves are for different temperatures :

15°C - ▪

25°C - •

These curves are derived from Figs 20 and 21 respectively. (see page 29 and Table 17)

the 'observed

e two curves

and 21

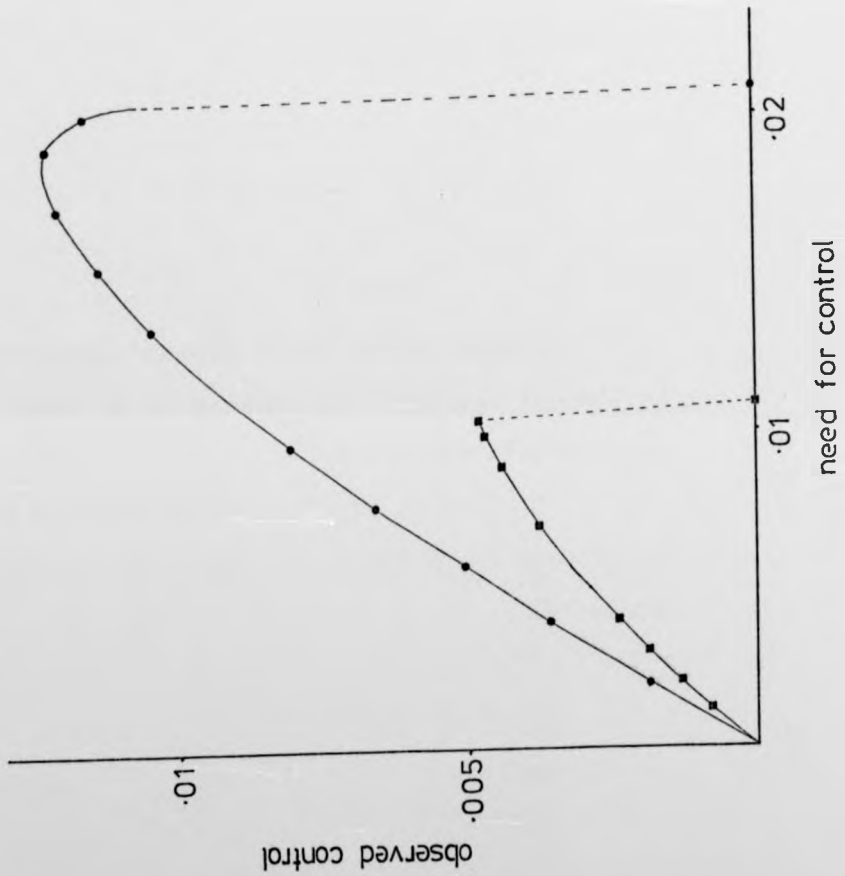

Figure 25

'Observed control' vs the 'need for control'. These are plots of the initial linear sections of the graphs presented in Figs 23 and 24.

The lines are fitted by eye. One line fits the 10 and 25°C data whilst another is fitted to the 5 and 15°C information.

5°c - □

10°C - ■

15°C - ○

25°C - ●

ntrol'. These

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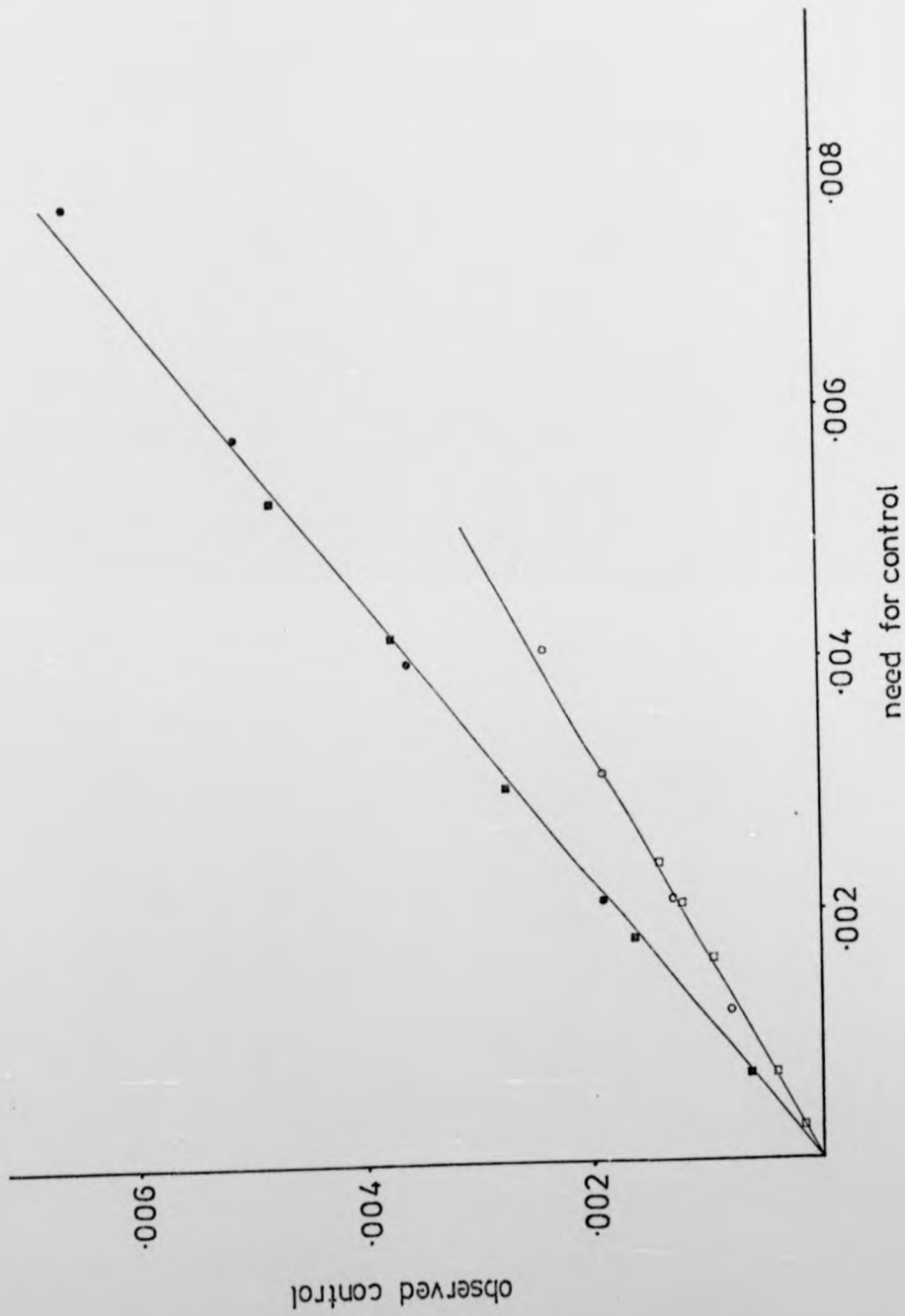
fits the 10

and 15°C



4. Discussion

4.1. Allometric Growth : The relations between organic carbon , length and dry weight - and environmental effects on these.

The relationships between organic carbon, dry weight and length have been thoroughly defined. Fig 5 shows the relation between length and organic carbon ($c = A\, l^m$) . A linear (log l vs. log c) version of this is presented in Fig 4. This line is statistically significant at the 99% level. The equation is :

$$\log c = 2.3078 \log l + 1.0135$$

This relationship is based on data pooled from all of the separate log c vs. log l regression lines produced using P. jenkinsi grown under different conditions of salinity and temperature (Table 1). It has been shown that these lines are statistically different and that pooling the data, as in the single line above is,strictly speaking, invalid. Thus the conditions of salinity and temperature in which the animals were grown had a significant effect on the relation between shell length and total organic carbon content. However, no obvious trends related to temperature or salinity have been discerned (Table 3).

The primary aim of producing these length-carbon regressions was the conversion of the growth results, measured in length,to carbon values. Since animals grown under different conditions appear to exhibit different conversion relationships,the pooled data line could not be used. Thus each set of length - growth data was converted

to carbon - growth using a length - carbon regression line produced under the same conditions of temperature and salinity.

The relation between dry weight (total) and organic carbon is a simple linear one. This is to be expected since they are both mass based values. The regression equations as determined under different combinations of temperature and salinity are presented in Table 4. These relationships show some temperature related trends. Table 5 shows the correlations between the slope of the dry weight - organic carbon regressions and the temperatures at which the animals were grown. In all salinities except 14°/oo these correlations are highly significant.

The general implications of these results are that animals grown under different salinity and temperature regimes are likely to have different shell and or tissue weights and organic carbon contents when they achieve a given length.

4.2. The Value of Organic Carbon as a Measure of Growth.

There are a number of parameters the measurement of which provides an index of the growth of molluscs such as P. jenkinsi. These include various linear shell measurements; length, width and aperture size; total dry and wet weight; tissue and shell dry and wet weights, calorific value and organic carbon content. These all emphasise certain aspects of growth and so they have different degrees of value to the physiologist. Further, different restrictions apply to the use of these parameters which affect their practical employment.

A large proportion of these methods provide results which are dominated by the shell. These are total wet and dry weight and all external linear measurements. Such parameters obviously have

some use since they have been employed by malacologists through the years (Table 18). The aspects that favour them revolve around their ease of application. They are easily measured with simple unspecialized equipment. All but dry weight have the added advantage that they are non - destructive : the animal need not be killed and so consecutive measurements on the growth of specific individuals are possible. Shell length has been employed in growth experiments by the author for this reason. However, such shell dominated measures of growth are of restricted value. They are useless in comparative physiology and ecology due to the existence of interspecific differences in shell geometry (see Calow 1975) and they are based on the measurement of a lifeless, secreted component of the animal. The shell is comparatively massive and whilst it is possible in larger molluscs to separate the 'biologically interesting' tissues from the shell this is extemely tedious in small gastropods such as P. jenkinsi. What is required is a method of evaluating growth which is rapid, accurate and which gives a result of ecological significance.

Bomb calorimetry provides an accurate estimate of growth, in terms of calorific value, which is the most universally comparable measure available and that usually employed in studies of ecological energetics. This method is however quite slow,whilst organic carbon analysis is rapid and also gives an accurate result. As has been demonstrated the scale of the method can be specifically adapted to the size of the organisms involved. It is most useful for small animals since on a large scale the volume of chromic acid involved makes the method ungainly.

Organic carbon is a reasonably good interspecifically

Table 18

Some growth studies on molluscs : author, date, species and method used for measurement.

uthor, date, species

AUTHOR	DATE	SPECIES	MEASUREMENT
Berrie	1966	Lymnaea stagnalis	shell length
Cole	1956	Cardium edule	shell length
Cole & Waugh	1959	Oysters	shell diameter
Foster	1932	Sphaerium	length, width & thickness
Foster	1936	Polyyra	shell size
Havinga	1928	Oysters	weight
Loosanoff	1954	bivalve larvae	shell length
Nomura	1926ab	Spherium heterodon	length, width & weight
Nomura & Sasaki	1928	gastropods	" " "
Prinsloo & vanEeden	1973	Bulinus tropicus & Lymnaea natalensis	weight
Rothschild & Rothschild	1949	Hydrobia ulvae	shell length
Russell-Hunter	1953	Ancylus fluviatilis	shell length
Sewell	1924	fresh water and brackish molluscs.	shell dimensions

comparable measure of growth. However, care must be taken in the comparison of species with markedly different carbohydrate, fat or protein contents since these will tend to give different results when measured against glucose standards even if their actual organic carbon levels are identical (Russell-Hunter et al 1968). Thus whilst the method of organic carbon analysis is more easily applied than calorimetry more care must be taken in standardising the results for interspecific comparisons. Burky (1971) states that interpopulation variation in molluscs is such that the use of organic carbon analysis is necesary in intraspecific comparisons of growth. This is of especial interest when the growth of snails such as P. jenkinsi is analysed, since great variation in shell shape occurs in this species (see Appendix I).

A great deal of intraspecific variation has been noted in Hydrobia ulvae (Pennant) a similar snail to P. jenkinsi living in more saline waters (Muus 1967, Chatfield 1972). The existence of physiological races has been suggested for H. ulvae (McMillan 1948a, Fretter and Graham 1962). This is also possible for P. jenkinsi (Warwick 1952,69). McMahon (1975) discusses how the 'high degree of isolation in freshwaters and the great variation maintained in populations of freshwater snails make them suitable material for the study of physiological races.' This author employs organic carbon analysis in the evaluation of bioenergetic variation in three populations of Laevapex fuscus (Adams), a fresh water limpet. Limpets from different populations exhibit different carbon verses aperture length relationships. The aperture length verses dry weight relation also varied between these populations. Reasonably convincing circumstantial evidence for genetic differences between these populations was presented.

Work on P. jenkinsi (Tables 1 -5) indicates that such differences in length - weight - carbon relations in nature could be caused by environmental variation and its interaction with a euryplastic phenotype. There is no doubt of this in the laboratory studies on P. jenkinsi presented here, since all the animals were taken from a homogenous population at a single collection area.

Thus whilst genetically based differences in race - population physiology are important, some of the observed variation in biochemical composition and physiological activity, in animals from different geographical localities, must be attributed to environmental causes. Dare and Edwards (1975) discuss seasonal changes in carbohydrate, protein and lipid composition in mussels. They state that 'Seasonal changes in flesh weight and composition result from the storage and utilization of food reserves in relation to the complex interactions of food availability and temperature with growth and reproductive processes.' Considerable local variation in such interactions is likely in the fresh water environment. The three populations of L. fuscus studied by McMahon (1975) all showed increases in carbon content prior to winter. Burky (1971) reports a similar effect for Ferrissia rivularis (Say). Clearly, this will be induced by some environmental variation, temperature and photoperiod being likely causal factors related to the seasons. At all events seasonal changes cause differences in the biochemical organisation of these species. This is compatible with what has been shown for P. jenkinsi which appears to exhibit seasonal variation in its capacity for growth (see pages 20 - 23). Changes in the relation between dry weight and organic carbon content in P. jenkinsi are definitly correlated with temperature (at all salinities except $14^{o}/oo$). An animal grown in the cold with adequate food has a larger carbon content than a similar (weight) warm grown individual (Tables

2, 4 and 5). Thus with the approach of winter, as the temperature begins to fall, molluscs such as L. fuscus, F. rivularis and presumably P. jenkinsi lay down carbon stores (probably carbohydrate - Russell-Hunter et al 1968) in preparation for a period of general environmental stress.

Thus organic carbon analysis is a measure of biomass which is sensitive to environmentally caused differences in animals from natural populations. It provides a parameter which accounts for variation in the amounts of material stored by animals. Whether the deposition of expendable storage carbohydrates etc. should be regarded as'growth' is unclear. It is possible that some workers might prefer a more definiteand possibly less analytical measure than organic carbon, which avoids the variation exposed by this method. Whether a fat man has achieved more growth than a thin man of the same height is a matter of interpretation since fat deposits may be lost. Such impermanent reversible growth as that involved in fat deposition is of a qualitatively different nature to the growth of the skeleton measured as height in humans and perhaps as shell length in molluscs. One could have two snails one of which was smaller in linear terms than the other. However, this smaller animal, because of its environmental history may have large carbohydrate stores, making it in terms of organic carbon, larger than its linearly bigger companion. Which has grown more? Clearly the growth parameter employed must depend on what is required from the work. If this is primarily a growth study then more than one parameter should be employed in order to give a balanced view.

The fundamentally different nature of these parameters can lead to different interpretations of results. For instance, an individual P. jenkinsi 2.5 mm. in length has a carbon content of about 85 ug. (Fig 4). Another, twice this length contains 425 ug.

(approx.). It is five times the size of the first animal when growth is measured on a carbon basis. Similar differences may be observed between length and weight.

Thus different measures of growth give different interpretations (1) because of a fundemental disparity between dissimilar linear and mass based measures and (2) because of differences in their capacity to vary and the nature of the variation. The ecologist concerned with energetics needs infomation in a 'universal' form which provides growth indices in energy related terms. Organic carbon analysis is certainly an attractive compromise between calorimetry and the measurement of weight or length.

A final consideration concerns the use of shell length in molluscan growth studies. Gastropods grow through a spiral and not a linear path. Thus a measure of shell length bears a complex relationship to the length through which the animal has actually grown. Thus shell length is a deceptively simple growth parameter which bears a'complicated' geometrical relation to the'real'growth of the mollusc. This relation varies with shell geometry and hence between species (see Calow 1975).

The value of organic carbon analysis in growth studies is clear. The method provides information of an analytical and physiological nature of more use to the ecologist than the conventional parameters; length and weight.

4.3. Growth and the Physiological Ecology of P. jenkinsi

P. jenkinsi may be found in waters varying from fresh to approximately 24°/oo salinity (Fretter and Graham 1962, Clay 1967, Muus 1967). Clay states that the species 'thrives' in the salinity range 3 - 10°/oo whilst Muus observes that it is numerous and dominant up to about 7°/oo and 'sporadic' up to 24°/oo. Warwick (1969) notes that type A P. jenkinsi may live in 'strongly brackish' water, about 19% sea water (7°/oo salinity). The general impression is that the species has a strong distribution in fresh water and in saline water up to approximately 7°/oo. Above this salinity the distribution is increasingly sporadic.

The species exists on all types of substrate ; running and still water, temporary pools and salt marshes under both steno and eurythermal conditions (Clay 1967). It is also found under conditions of low oxygen. Thus P. jenkinsi is highly tolerant of environmental variation (Warwick 1947, Bondesen and Kaiser 1949, Heywood and Edwards 1962).

P. jenkinsi achieves maximum growth rates at a salinity of 14°/oo at all temperatures between 5 and 30°C (in both length and carbon terms - k_e^l and k_e^c - Figs 12 and 13a). Growth is also maximal at 25°C for all salinities. Thus 25°C and 14°/oo salinity gives the highest growth rate of any combination of salinity and temperature. These optimal conditions for growth may be considered moderately high extremes in relation to the normal species distribution in Britain. The optimum salinity for growth is outside the 0 - 7°/oo range where the species is often 'numerous and dominant'. The optimum temperature for growth coincides approximately with the maximum that the species will experience in a natural habitat in Britain (see Macan 1974).

Thus growth is not maximised under the conditions generally experienced by the species. Kinne (1971) declares that it is unusual for a species of aquatic invertebrate to exhibit maximum growth in salinities different from those in which maximum densities of population occur in nature. The growth responses of the species could be a relic of an evolutionary background in warmer (New Zealand) bracki sh waters (Bondesen and Kaiser 1949, Hubendick 1950, Winterbourn 1969,70ab,72). However it may be that the growth physiology of P. jenkinsi has been adapted in order to fully exploit the range of favourable salinity and temperature conditions found in temperate habitats, whilst retaining a highly successful tolerance of sub - optimal environments. Thus within the bounds set by the species distribution in Britain increases in salinity and temperature nearly always give increases in growth rate : the peak is (presumably) rarely reached. The main distribution of P. jenkinsi extends to lower salinities than those for maximum growth and 25°C is rarely experienced. The physiological apparatus supporting growth is stable and increasingly active up to about 26°C at all salinities(Figs 15 and 16). At temperatures above 26°C the growth rate declines.

P. jenkinsi is successful in fresh water with a relatively low growth rate. Whether the increase in growth rate in saline conditions is a necesary adaptation is unclear. It is possible that this compensates for the depressant activities of some additional environmental stress present in the estuarine environment.

The species penetration into brackish water extends beyond the point where growth is maximal. However, as shown in Figs 12 and 13a growth is still rapid at 21°/oo and so a decrease in growth rate is

probably insufficient to restrict the main population distribution to salinities below this level. A decrease in reproductive activity is more likely to prevent expansion into higher salinities. According to Kinne (1971) reproduction is less tolerant of 'extreme' salinities than growth, which in turn has a narrower range than survival (in aquatic invertebrates). Information concerning P. jenkinsi confirms this view. Bondesen and Kaiser (1949) progressively increased the salinity in which P. jenkinsi were living. Reproduction ceased at 28°/oo and was severely reduced at 16°/oo. Duncan (1966) found that breeding rates were low above 12 and 18°/oo for animals taken from fresh and brackish water populations respectively. She considered 18°/oo to be the border salinity between easy and difficult osmo - regulation.

There is no information in the literature concerning the reproductive response of P. jenkinsi to temperature. However, its existence in a thermal spring at 19°C (Warwick 1947) indicates that reproduction is possible at elevated temperatures in nature. Observation of the animals used in the growth experiments showed that those maintained at 10 and 15°C consistently produced young. Those at 5°C were reproductively inactive and at 25°C only occasional individuals had young. Thus it seems likely that the species is fecund in the approximate range 10 - 20°C.

Thus the optimal conditions for growth do not coincide with those for reproduction. Reproductive limitation will restrict the ability of populations of P. jenkinsi to survive in habitats with consistantly high salinities and temperatures where migrant individuals could successfully grow. Occasionally an individual with a more tolerant reproductive physiology might find itself in such an extreme habitat and as a result extend the local range of the population.

The optimum growth rate for individuals of a species must be one which enables the animal to produce the largest number of young which are themselves able to achieve reproductive maturity. It seems that P. jenkinsi takes advantage of any favourable conditions presented to it by growing more quickly. However, the results indicate that some endogenous constraints may restrict this response so that small P. jenkinsi only achieve rapid growth in the spring when both the weather and this internal control is favourable. A possible reason for this would be the maintenance of a population structure such that there are always small animals present. These smaller animals may resist extreme winter coditions more successfully than adults (Taylor 1960). There is some evidence that larger P. jenkinsi are more susceptible to low winter temperatures (Lumbye and Lumbye 1965). The growth of P. jenkinsi in the field is not well presented in this paper but it appears that animals born in the summer achieve some growth in the autumn. Growth ceases in the winter and begins again in the spring, the animals achieving reproductive size in the summer. These large animals are unlikely to survive their second winter.

Thus animals born in the summer, which appear to have low growth potential at this time, will tend to over-winter as small individuals, during which time they lose the growth restraint so that when conditions become favourable in the spring, they can grow quickly. Five weeks exposure to 5°C failed to increase the low growth potential of small P. jenkinsi removed from the River Ore in the summer (Table 11). It is possible that other factors such as photoperiod are involved in growth control.

Whilst Taylor (1960) states that it is 'commonly observed' that young small animals are resistant to extremes of temperature, Klekowski and Duncan (1966) have shown that juvenile P. jenkinsi

are very resistant to high salinities. Thus it appears that the maintenance of small individuals in a population will confer a high degree of tolerance to environmental fluctuation. Klekowski and Duncan (1966) found that juvenile P. jenkinsi were 'healthier', more active and darkened more quickly in saline media. Their experiments were not sufficiently sensitive to detect differences in growth at various salinities. The animals grew from 0.6 to 0.7 mm. in length in 55 days. This is an extremely slow growth rate (growth temperature was 21°C) even considering that at this size the animals are in the early slow phase of the sigmoid growth curve. This could have been due to the action of some endogenous growth restraint as experienced in growth experiment 2a (see pages 19 - 23 and Table 10). Alternatively such poor growth could have resulted from the fact that the animals were taken from a laboratory population. The growth of such animals is often poor.

Those P. jenkinsi maintained in saline media by Klekowski and Duncan (1966) survived exposure to 38°C for 13 hours whilst those in fresh water succumbed. Activity was 50 - 100% higher within the mid - range of salinity. Thus it appears that P. jenkinsi is primarily adapted for life in mildly brackish waters; growth, activity and reproduction all being stimulated by a moderate elevation of salinity over fresh water. That the species is successful in fresh water indicates that the constraints on life in this environment are not severe enough to restrict it despite some reduction in physiological performance.

The parthenogenetic mode of reproduction exhibited by P. jenkinsi has a great deal of influence on the ecology of the species. White (1970) states that 'Well studied cases of parthenogenesis tend to support the view that adaptive evolution under conditions of parthenogenetic reproduction is limited. A parthenogenetic form may be adapted to a

new ecological niche at the time of origin and may be very successful at conquering that niche. But it is unlikely to undergo much subsequent diversification adapting it to further environments.' However, a parthenogenetic animal is greatly favoured in colonisation where a sexual animal would have great difficulty due to the low probability of discovering a mate in a locality new to the species (Tomlinson 1966). This is of especial importance to a sedentary species like P. jenkinsi. Thus the situation arises where an animal which is conservative in evolution is exposed to new habitats; in the case of P. jenkinsi, as a result of passive dispersal (Hubendick 1950). Thus the fact that P. jenkinsi has successfully colonised a large variety of aquatic habitats in Britain (and in Europe,Hubendick 1950, Doby et al 1965) implies that the species, when it origi nally assumed the parthenogenetic mode of reproduction, was tolerant of a wide range of environmental variation.

According to Kinne (1966) estuaries, because they are habitats with a high general level of stress, provide a refuge for species with good physiological adaptability but poor competitive power. Such habitats with a high degree of salinity fluctuation promote evolution to cope with this but do not promote evolution in general : 'High genetic salinity tolerance and evolutionary conservatism often go hand in hand.' If this is true , estuaries provide environments which do not demand species adaptability on an evolutionary time scale whilst requiring individual physiological flexibility on a scale measured in hours. Thus estuarine habitats may be suitable for parthenogenetic animals such as P. jenkinsi which possess a high degree of tolerance to stress but whose genetic system limits them so far as new evolutionary development is concerned.

Whether this argument is compatible with the fact that the

estuaries that exist now were only formed some 3000 years ago is unclear. This emphasises the long term instability of specific estuarine habitats. With the rise and fall of the land masses and sea levels due to glaciation the sites where rivers meet the sea must change. Many estuarine species may have evolved recently or may be evolving currently (McLusky 1971).

Fresh water provides a variety of habitats many of which have been colonised by P. jenkinsi (Clay 1967). All of these are generally more stable than the estuarine environment in the short term since they lack the constant flux of physical and chemical conditions due to the tides. P. jenkinsi has been successful in increasing its range in fresh water since the begining of the century (Hubendick 1950). However, the ability of P. jenkinsi as opposed to a similar sexually reproducing animal to survive in the long term is uncertain. Local populations of P. jenkinsi exhibit some signs of instability. Clay (1967) and McLeish (per. comm.) both note the sudden arrival and disappearance of populations. In the winter of 1972 - 73 the population of P. jenkinsi in the River Ore at Thornton disappeared only to return early in spring.

Burky (1971) and McMahon (1975) both comment on the existence of geographic physiological races within species of freshwater molluscs. Further, individuals within such populations exhibit wide phenotypic flexibility. Russell - Hunter (1970) states that there appears to have been strong selection for the capacity to vary. Non - migratory freshwater animals exhibit flexibility at both the individual - physiological and population - genetic levels. There appears to be more variation between populations than within them, which demonstrates race development. When considering such euryplastic organisms this

should express itself as a difference in the average of the particular characteristic varying between populations. Some papers concerned with both racial and individual variation in aquatic molluscs are : Hamai 1934, Moore 1936, Peters 1938, Diver 1939ab, McMillan 1948a, Wright and Ross 1965, Meenakshi et al 1969, Richards 1970 and Chatfield 1972.

Such individual and population flexibility is important in freshwater (and presumably estuarine) environments since they are both spatially and temporally heterogenous. The duration of freshwater habitats is less than that of terrestial or marine habitats. A species inhabiting freshwater must be capable of evolution in response to environmental change in both the spatial and temporal plane if conditions approach the limits of its phenotypic capacity.

Since parthenogenetic animals have limited adaptive potential they are more likely than sexually reproducing species to become locally or totally extinct. Isolated groups of P. jenkinsi do not constitute populations in the evolutionary sense. Evolution in such species occurs at the individual or clone level. In contrast to sexual animals evolution is not based on the interaction of individuals in a population - mating and producing young on which selection acts. Any parthenogenetic individual possesses a certain degree of plasticity enabling it to survive under a variety of conditions. However, further adaptation to environmental variation beyond the current limits is unlikely. In parthenogenetic species phenotypic selection is less likely to result in genetic evolution and the formation of geographic races or new species.

There is a fundamental dichotomy in the evolution of species. As Kinne (1971) has outlined, selection at the individual level will tend to result in animals becoming maximally adjusted to their particular habitat. This can only be achieved at the expense of variability in the

population since this is based on the non - perfect adjustment of at least some of the individuals (this argument assumes that the individuals in a population all live in a uniform type of micro - habitat within their general environment). A population which is too uniform will be unable to produce individuals capable of surviving environmental change. Maynard - Smith (1966) states that the 'advantage of the sexual process is that it increases the range of potential variation in a population and therefore its evolutionary plasticity.' Sex provides a way of combining and exposing favourable mutations, which origi nally occured in different individuals, in a given animal(s). Parthenogenetic animals are therefore less likely to produce new variation. They must rely on a fundementally wide tolerance presumably inherited from a sexual ancestor. Mayr (1963) takes the view that all examples of parthenogenesis are recent and secondarily derived from sexual precursors. Patil (1958) takes this view of P. jenkinsi.

In parthenogenetic animals mutations, which are usually recesive, are seldom exposed to selection since they do not achieve homozygosity(due to the absence of recombination). Parthenogenetic species will accumulate such mutation and become heterotic. In addition to heterosis at single loci they can tolerate large chromosome irregularities since the chromosomes do not have to pair in the absence of meiosis. White(1970) states that parthenogenetic animals may have inherited a large amount of heterozygosity as a result of origin through interspecific or interracial crossing. He expresses the view that parthenogenetic species possess genetic systems which 'exploit the advantages of heterosis and adaptive polymorphism.' Such species usually exhibit only a single type or a limited number of cytogenetically identifiable polymorphs. They do not show the chaotic variation which might have been expected since accumulated

mutations are seldom expressed. Whether P. jenkinsi is polymorphic is as yet unclear. The work of Sanderson (1940) and Warwick (1952,69) suggests that it is.

The existence of different polymorphs would make the 'species' in so far as it could be regarded as such (see Appendix I), a more diverse and viable unit since the different genotypes would presumably be adapted to different (if considerably overlapping) niches within the same general habitat. Thus they would be likely to have different tolerance ranges and levels of performance etc. (Reddingius and den Boer 1970). This work has shown that P. jenkinsi of a single type (strain A - T. Warwick - per. comm.) possess a wide range of tolerance to temperature and salinity. Whilst there was some individual variation in performance under set conditions this was not great. It remains to be seen whether animals from different populations show genetically determined physiological differences to these. Todd (1964) notes some osmotic differences between strains of P. jenkinsi (as defined by Warwick 1952, 69). The work of Duncan (1966) may be interpreted as showing differences in respiration, activity, mortality and reproduction in P. jenkinsi from different fresh and brackish water populations. Duncan notes a high degree of individual variation in respiration which explains why the population differences were not statistically significant. If the view of parthenogenetic species proposed by Mayr and White is accepted such apparently random individual variation must be regarded as phenotypic. As yet no convincing physiological or cytogenetic evidence has been presented for the existence of specific recognizeable races or the association of physiological differences with morphological types.

4.4. Comparative Physiology of Growth : Temperature and Salinity Effects.

The aim of this section is to establish generalizations and to compare the environmental physiology of P. jenkinsi to that of other species. It is hoped to illustrate the extent to which P. jenkinsi, due to its proposed evolutionary background, exhibits unusual responses.

Prinsloo and van Eeden (1973) state that the optimum temperatures for the growth of Bulinus tropicus (Krauss) and Lymnaea natalensis (Krauss) are 25 - 27 and 15°C respectively. These snails are native to 'South Africa where summer temperatures are generally high and the available habitats are subject to intermittent drying up.' On the basis of growth rate P. jenkinsi would seem to be as well adapted to high temperatures as these African species and in fact better adapted than L. natalensis.

Michelson (1961) examined the effect of temperature on the growth of the tropical snail Australorbis glabratus. Growth was most rapid at 30°C and progressively slower at 25, 20, 15 and 5°C the latter being lethal within a week. These results indicate adaptation to a generally warmer environment than that experienced by P. jenkinsi which survives 5°C for long periods and grows fastest at 25°C.

Michelson also showed that whilst growth was maximised at 30°C reproduction was inhibited at this high temperature. This is similar to the response in P. jenkinsi where reproduction is inhibited at the peak growth temperature of 25°C. Calabrese (1969) showed that the coot clam Mulinia lateralis (Say) exhibits a peak of growth at a temperature beyond that which begins a decline in reproduction.

Kinne (1971) states that the range of salinity tolerance is

different for different processes. Thus survival has a greater tolerance than growth which has a wider range than reproduction. A similar relation occurs for temperature (Kinne 1970). This may be true but it takes no account of shifts in range, the peaks and ranges of activity of different physiological processes being displaced from one another. This has been shown for both temperature and salinity in P. jenkinsi (growth is maximised at 14°/oo whilst Duncan -1966, has shown that reproduction peaks at 3 - 6°/oo) and for temperature in Australorbis glabratus and Mulinia lateralis.

Vaughn (1953) concluded that the optimum temperature for the growth and development of the temperate species Lymnaea stagnalis appressa (Say) was between 16 and 20°C. Initially growth was faster at 24.2°C but mortality was significantly increased at this temperature. After two weeks snails growing at 24°C+ suffered a decline in growth whilst that of animals below this temperature continued to increase. Snails at 32 and 36°C died within a week whilst those at 28°C died more slowly. Vaughn proposed a biological zero for the species at about 11°C below which growth was virtually totally inhibited. This corresponds to about 5°C for P. jenkinsi which appears to be comparatively eury - thermal.

Mytilus edulis (L.), another temperate zone species, was found to grow maximally between 17 and 20°C. Feeding and growth continue at and below 14°C but at a much lower rate. The mussels were able to feed over the range 7 - 26°C (Coe 1948).

Both of these temperate species exhibit lower temperature maxima than P. jenkinsi whilst the tropical species A. glabratus has a higher peak growth temperature. P. jenkinsi has a similar maximum growth temperature to B. tropicus and exceeds that of L. natalensis.

Kinne's (1970) review includes references to temperate species which exhibit high maximum growth temperatures in the range 25 - 30°C. This may not therefore be unusual. Possible reasons for this have been discussed (page 38).

Kinne (1960) shows that the euryplastic fish Cyprinodon macularius (Baird and Girard) has different salinity optima for growth depending on temperature. Thus at lower temperatures pre-adult growth is fastest in fresh water but at higher temperatures it is most rapid at 35 and 55°/oo salinity. It is stated that 'the effects of a given temperature depend on the salinity and vice-versa : that the combination of temperature and salinity is of basic importance.'

P. jenkinsi does not experience any shift in the salinity optima for growth with temperature : the pattern is the same from 5 - 30°C but is accentuated at higher temperatures. However, particular combinations of salinity and temperature have unique importance since they exhibit specific and varying (with different combinations) synergistic interaction. The degree of this interaction may (at present) only be determined experimentally since it is not readily accessible to prediction. The patterns of factor interaction are probably susceptible to subtle modification. Other factors may influence the synergistic reaction between salinity and temperature and may be involved directly in other similar relations. Thus physiological performance may be susceptible to modification due to a range of synergistic effects some of which will vary seasonally. Such interactions may be of great significance to the ecology of a species.

Synergistic interaction is possibly of greater importance in fresh water and estuaries than in other environments due to the large degree of isolation of suitable species habitats and the high phenotypic plasticity shown by the inhabitants. Thus in freshwater and estuarine habitats such animals will experience and tolerate a wide range of

different combinations of physical and chemical factors. This will provide opportunities for synergism to occur.

The existence of synergistic interaction indicates that organisms such as P. jenkinsi integrate the environmental information that they receive and tend to respond to the environmental whole rather than to isolated components. Thus P. jenkinsi reacts to salinity and temperature as bimodal aspects of its experience rather than separate unrelated effects.

4.5. Growth : Mechanisms of salinity and Temperature Effects

4.5.1. Introduction

The effects of salinity and temperature have been discussed within the context of the physiological ecology of the species. It remains to describe the mechanisms by which these environmental variables modulate the physiology of animals such as P. jenkinsi .

Growth is not a simple process. A measurement of growth is a measurement using a single simple parameter to evaluate the net result of a vast complexity of biochemical interaction. Indeed, it could be stated that virtually every biochemical (and hence physiological, structural and behavioural) reaction ever performed by a given individual contributes in some positive or negative fashion, via the distribution of energy and material resources, to this simple parameter. However, it is clear that some components of life will have much more bearing on growth performance than others.

The growth equation attributed to Bertalanffy (1957), despite all the criticism levelled against it,(Hemmingsen 1960, Hubbell 1971, Calow 1973 - see section 4.6.) gives a clear starting point for a discussion of the mechanisms underlying growth :

$$dw/dt = hw^m - dw^n$$

where - w = weight, h = constant of anabolism, d = constant of catabolism, m and n indicate that anabolism and catabolism are proportional to some powers of body weight.

Thus growth is the net outcome of anabolic and catabolic processes and is seen here as a passive result of their interaction. Any attempt to

describe the basis of environmental effects on growth must account for changes in both anabolism and catabolism since both the synthesis of cell building material and the production of useable energy supplies have essential and linked contributions to make to growth. Thus growth responses to environmental factors are here viewed as resulting from effects on the underlying metabolism. Further if growth is viewed as a controlled process (Hubbell 1971, Calow 1973) direct effects via the control systems will have to be defined. Calow has shown that Planorbis contortus (L.) responds to periodic food shortages by eating more when food is made available. Thus, in this case, behavioural control moderates the potential effect and tends to maintain growth at the optimum rate. The growth of P. jenkinsi has been shown to be controlled with respect to salinity (pages 28 and 29).

Any explanation of the fundamental mechanisms which underlie the observed variations in the growth of P. jenkinsi, with respect to differences in salinity and temperature, must be speculative due to a lack of basic knowledge concerning the biochemistry of the species.

4.5.2. Temperature Effects on Growth : The Arrhenius Model

Kinne (1971) has stressed the importance of investigating the effects of environmental variables on growth and relating these to the sub-individual level of organisation. Regarding salinity he states that effects on growth rates are of 'considerable theoretical interest as they are closely related to regulation of water and salt, permeability, active trans port and other basic physiological phenomena at the organismic, tissue, cellular and molecular levels.' Temperature has similar profound effects.

Arrhenius plots prwide a link between growth data and the existence of underlying kinetic and metabolic effects. Farrell and Rose (1967) employed Arrhenius plots in the comparative analysis of the growth of populations of thermophilic, mesophilic and psychrophilic bacteria. The growth of these organisms occured over different temperature ranges and where they did overlap the growth rates were quite different. These differences were presumably adaptive since they conformed to expectations based on their environmental backgrounds.

Since growth is enzyme mediated and enzymes in vitro show similar Arrhenius plots to whole organism growth (Brandts 1967) it is tempting to compare the two and draw the obvious conclusion that the observed effects of temperature on growth are caused by enzyme - temperature interaction. However, Farrell and Rose (1967) caution against this interpretation on the grounds that growth is a very complex biochemical process and other effects might be the cause of these growth responses to the environment. The alternatives remain undefined.

Brandts (1967) working on the growth of the protozoon Tetrahymena pyrifornis with respect to both temperature and D_2O concentration produced a series of Arrhenius lines remarkably similar

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Brandts (1967) working on the growth of the protozoon Tetrahymena pyrifornis with respect to both temperature and D_2O concentration produced a series of Arrhenius lines remarkably similar

to those for the growth of P. jenkinsi (temperature and salinity) shown in Figs 15 and 16. Brandts draws analogies between the known responses of pure enzymes and the behaviour of intact - organism physiology. The responses of enzymes to D_2O and temperature are cosistent with those exhibited by whole organisms.

The Arrhenius plots include a linear section where the growth of T. pyrifornis shows a response to temperature similar to that of pure chemical (or enzymic) reactions accelerated by increased thermal - kinetic energy. This is bounded by non - linear sections where the system breaks down due either to enzyme inactivation or some undefined breakdown in coordination etc. The temperatures (high and low) at which breakdown occurs are not affected by the concentration of D_2O. Thus the stability of the growth system components is relatively unaffected by D_2O as is the stability of pure enzymes. The rate of growth is however affected by D_2O level.

Fig 15 shows how the growth rate of P. jenkinsi is affected by salinity whilst the high temperature breakdown point (P. jenkinsi does not exhibit an obvious low temperature breakdown) is independent of salinity. Thus the temperature sensitive components of growth physiology,(enzymes, polynucleotides and hormones etc.) whilst being affected by salinity sufficiently to alter their rate of activity, must be immune to any degradative effects.

Narasimhan and Krishnamoorthy (1975) have demonstrated similar temperature - salinity effects on the anabolism of a species of euryhaline crab. Glycogen production in this animal shows a similar pattern of response to that of the growth of P. jenkinsi ; the rate of synthesis being both temperature and salinity dependent, whilst the point of breakdown wasunaffected by salinity. Thus enzyme effects are further implicated in the relation between growth, salinity and temperature.

It is to be expected that enzymes (intra and extracellular) should play a central role in the responses of organisms to pervasive environmental variables : enzymes are both crucial to all aspects of life and are known to respond *in vitro*. Thus since it is known that enzymes in general respond to temperature (Read 1964, Brandts 1967, Hazel and Prosser 1970, Hochachka and Somero 1973) those of poikilotherms *in vivo* are bound to be affected. Similarly effects of salinity and ions in general have been noted (Dixon and Webb 1958, Hochachka and Somero 1973, Gilles 1975b) and so animals which do not maintain constant cellular ionic levels will experience changes in various enzyme catalysed reactions. Hochachka (1967) demonstrates the involvement of both changes in (1) the activity of existent enzymes and (2) the cellular apparatus necesary for the synthesis of new enzymes,in the adjustment of fish metabolism to new temperature regimes.

4.5.3. Enzymes, Metabolism and Growth : Temperature Effects.

The work of Hochachka and Somero (Hochachka 1967,68,. Hochachka and Somero 1968,73,. Somero 1969 a & b,. Somero and Hochachka 1969.) has been particularly successful in showing how biochemical adaptation enables organisms to maintain an integrated adaptive metabolism when exposed to variation in envirionmental temperature. The principal weapon employed by poikilotherms is the ability to change the enzyme - substrate affinity of enzymes so as to adapt them to the current situation. Thus if it were desirable for a reaction to remain constant (in rate) independent of temperature the E - S affinity would decrease in proportion to the increase in kinetic energy and vice - versa. A range of control is possible (under, perfect and over-compensation) depending on the degree of change in E - S affinity in relation to a given change in temperature. Some enzymes show no compensation (Q_{10} 2) whilst others exhibit inverse or paradoxical non - compensatory changes in affinity (Hazel and Prosser 1970). It is intuitively reasonable that cells with their vast complexity of biochemical interactions should require a range of control responses in order to maintain a viable organisation. Whilst many enzymes will show normal (partial - perfect) compensation for low kinetic energy availability in the cold, enzymes involved in certain degradative processes show over-compensation. Thus when the temperature rises they operate at a rate which is faster than the stimulation due to kinetic energy alone would allow for. This is adaptive and removes excesses of solute material 'waste' resulting from an increased level of metabolism (Hazel and Prosser 1970). Thus, because control of some aspects of metabolism is not perfect certain enzymes have been specially adapted to maintain a

viable intracellular environment.

Hochachka (1968) has shown how differences in enzymes at branch points in metabolism cause changes in the carbon flow through various processes as a result of differences in the temperatures to which the enzymes were previously exposed. Genetically controlled changes in enzyme character and quantity will define the nature of physiological responses to temperature. Rao (1967) has produced a scheme outlining changes in metabolism following cold acclimation.

Kinne (1964) remarks on the fact that high - temperature tolerance is often associated with a low metabolic rate. The basal metabolism of intertidal molluscs has been shown to be relatively independent of temperature (Newell 1964,66,67,69 & 73a. Newell and Northcroft 1967, Newell and Pye 1970 ab, 71ab. Newell and Bayne 1973, Pye and Newell 1973). Hochachka and Somero (1973) speculate on the role of substrate concentrations, in relation to enzyme - substrate affinity, in these processes. Enzyme - substrate control is most effective when the substrate concentration is low. Thus if this mechanism is of importance then the maintenance of a viable metabolism will be easier in a relatively inactive animal with low levels of substrate. The results of the work of Newell and his co - authors are consistent with this theory.

A growing animal necessarily has an active metabolism. The growth rate of P. jenkinsi has a Q_{10} of 2-4 over various parts of the range 5-25°C. There is no consistent evidence for a temperature independent growth response although at 0°/oo salinity there is no increase in growth between 10 and 15°C. At all other salinities the Q_{10} for this range is about 2. An active metabolism due to growth implies generally high substrate concentrations but this does not mean that E - S affinity control is necessarily ineffective. If natural selection had favoured

temperature independent growth then it seems reasonable that evolutionary constraint would have resulted in the adaptation of E - S affinity responses in a suitable manner. Since animals possess mechanisms which could render growth related active metabolism independent of temperature why hasn't evolution for such a stable system occurred? The response of the growth of P. jenkinsi to temperature will reflect the ecological requirements of the species. It would appear that the best evolutionary strategy involves making maximum use of periods of high kinetic energy by allowing this to stimulate metabolism above the less active level maintained in the cooler months of the year. Thus animals will tend to grow in the warm summer months when the high temperatures favour metabolic activity and large quantities of food are concurrently available .

It is a truism that animals will only grow when conditions are favourable (for growth). What conditions are favourable will have been defined by the evolutionary interaction of the species and the environment. Different species find different conditions favourable. A temperature which is adversly cool for a temperate zone species may be highly favourable for the growth of a 'similar' arctic species. In a seasonless uniform environment animals would presumably grow at a uniform rate or at least would be independent of the environment and reflect only endogenous requirements and changes. They would not experience changes in the favourability of their habitat. A species introduced into such a habitat would presumably evolve in order to make the prevalent conditions favourable. In a fluctuating environment where conditions are predictable (as are the conditions at the different seasons of the year) an organism could evolve to make the total range of conditions

(best - worst) favourable to growth or it could, and this is what has occured with poikilotherms such as P. jenkinsi, evolve so that only the better conditions available promote growth. The remainder only support maintenance activities or a reduced level of growth. Obviously a sufficient period of the favourable conditions must be available if the species is to survive in a given habitat. When evolving, organisms appear to have a 'choice' about whether or not to grow and reproduce very quickly in the short period when conditions are very favourable or whether to spread the period of activity into less favourable times of the year and by doing so eliminate the need for very rapid physiological activity. Thus the conditions which are favourable and the period for which they must be available will vary between species.

Organisms such as P. jenkinsi adopt an exploitive attitude to their environment. When conditions are generally more favourable (warm - tending to 25 ^{o}C) they will grow quickly but in winter at temperatures of about 5^{o}C growth is minimal.

4.5.4. Salinity : Osmotic Effects

Todd (1964), Duncan (1967) and Bryan (1963) have all analysed the osmotic behaviour of P. jenkinsi. The species is isoosmotic or slightly hyperosmotic from 4 - 18°/oo salinity. Below 4°/oo and (probably) above 18°/oo strong hyperosmosity occurs.

Todd could find no differences in the osmotic concentration of the haemolymph which could be correlated with temperature. The experiments were done at 5 and 15°C (mean winter and summer temperatures). Some confirmation and expansion of this work is necesary. It has been shown that different species under different conditions exhibit various osmotic responses to temperature (Segal and Burbanck 1963, Ballard and Abbot 1969, Tucker 1970).

Potts (1954) has shown that the amount of energy used by invertebrates for osmotic work accounts for only about 1% of their total average expenditure. Thus the energy required for osmotic activity is small and changes in this due to conditions are unlikely to provide an explanation for the observed differences in growth.

Despite the fact that energy contributions to osmotic control per se are unlikely to effect growth , the consequences of changes in internal ionic and osmotic conditions, resulting from external salinity change, may be far reaching. Since it has been shown that ions have important effects on biochemical systems (Dixon and Webb 1958, Bygrave 1967) it is reasonable to suppose that these require a relatively stable and controlled solute state for viable and integrated metabolism to occur.Indeed it seems obvious that subcellular organelles, cells, blood and the environment, is a series with a decreasing control of the ionic state. Krogh (1939) states that 'In the molluscs ionic concentrations within tissue cells are definitely different from those in the blood

and often much lower. This difference in ionic levels is osmotically balanced, in the tissue cells, by small organic molecules. The recent review by Gilles (1975) shows how different species in different conditions may have very different intracellular concentrations of ionic and organic (primarily free amino acids) osmotic effectors. Marine species generally have high levels of organic solutes presumably freeing them from the complex effects of high intracellular concentrations of ions. Kinne (1971) states that freshwater species have a much easier task in cellular ionic control than estuarine or marine animals. The primary quantitative task is the excretion of NaCl from the cells against a gradient. This will be easier with a higher content of organic solute contributing to the osmotic balance. Gilles (1975) argues that intra - cellular ionic control is probably the basic mechanism, control at the body fluid level being an extra which confers a new range of possibilities on the species. It is further argued that the role of amino acids in this is 'universal' and basic. Negus (1968) however failed to find significant levels of amino acid for osmotic control in Hydrobia ulvae.

Thus when organisms such as P. jenkinsi are exposed to different salinities there are concomitant changes in blood and cellular ionic and osmotic levels. Organisms must permit such osmotic and ionic changes in order to maintain reasonably constant cell and body volumes, so that damage to delicate membranes and membrane located enzyme systems, is minimised. Thus the organism has to change its osmotic concentration quickly to avoid damage due to excess uptake or loss of water whilst protecting its metabolism from changes due to ionic variation. Thus changes in the levels of relatively innocuous organic solutes would provide organisms with a simple solution to this problem. Avens (1965II) showed that H. ulvae does not gain or lose water when the external salinity is altered. They explain this on the basis of

very rapid ion movement reducing osmotic differences between the cells and the medium. It is an interesting observation that small snails would find rapid ion exchange easier than large ones and that estuarine gastropods (including P. jenkinsi) tend to be small (Avens and Sleigh 1965 I).

Thus it is possible to conclude that the cellular biochemistry of molluscs such as P. jenkinsi experiences a modulated effect when external salinity is altered. The nature and mechanism of this effect (s) is at present unclear.

4.5.5. Physiological and Biochemical Effects of Salinity

That P. jenkinsi does not have perfect control over 'internal salinity' is obvious since all the species major physiological activities are, to some extent, salinity dependent. It has been shown that growth is significantly affected and Duncan (1966) has demonstrated changes in respiration activity, reproduction and survival correlated with salinity. Maximum growth and activity occur in the middle salinity range and it is not surprising to find that respiration is increased in this region.

Thus it is to the cellular and subcellular (biochemical levels of organisation that one must look for explanations of salinity effects. The observed physiological responses must reflect (1) the nature of the control systems at body fluid, cell and organelle levels and (2) the effects of the uncontrolled portion of environmental change on enzyme systems and cellular structures etc.

Dixon and Webb(1958) state that whilst cations tend to have highly specific effects on enzyme activities, anions elicit more general responses. Gilles (1975) in a study of salinity effects on succinic dehydrogenase activity demonstrated that it was the anions (Cl^-) that were , in this case , more important. It was shown how anions affect enzyme activity (succ. dehyd.) in the same order as their tendency to disrupt the structure of macromolecules ($Ac^- < Cl^- < Br^- < NO_3^-$). Thus it seems that these anions are affecting enzyme structure. This can have marked effects on E - S affinity and hence on activity.

Bygrave (1967) and Hochachka and Somero (1973) discuss the effects of ions on intermediate metabolism. Hochachka and Somero place special significance on the interaction between the glycolysis - Krebs system and amino acid formation. The presence of inorganic ions stimulates the formation of various amino acids the primary event being the stimulation

of glutamate production. There is a control'cascade'which is automatic. The cellular metabolism responds to ionic changes by producing concomitant changes in the levels of osmotically active free amino acids. This provides a biochemical basis for the work of physiologists on changes in amino acid levels in response to different salinities (Allen 1961, Duchateau, Bosson and Florkin 1961, DuPaul and Webb 1970, Virkar and Webb 1970, Brown and Stanley 1972).

Gilles (1975) shows how the thermosensitivity (inactivation) of glutamate dehydrogenase is increased by NaCl.

4.5.6. Temperature - Salinity Interaction

It has been shown that the middle range of salinity promotes a high degree of physiological activity in P. jenkinsi. This work has demonstrated that different combinations of salinity and temperature have different and variably synergistic effects (Fig 14) on the growth of the species. How such interaction between two completely different environmental variables occurs is unclear. In view of the previous discussion (section 4.5.5.) effects at the biochemical level seem most likely. However, although some work has been done on various aspects of molluscan biochemistry (Brand 1950, Martin 1961, Florkin and Scheer 1972, Goudsmit 1972, Voogt 1972) the level of understanding attained is lower than that for mammals or fish. Thus since the basic knowledge is lacking, generalization must be tenuous.

A primary problem is the importance and nature of facultative anaerobiosis in molluscs such as P. jenkinsi. Brand(1950) showed that snails resistant to anaerobic conditions (as is P. jenkinsi) do not contain significant levels of lactic acid. Thus it is either excreted, which is wasteful, or unusual biochemical mechanisms are operating in these species. Awapara and his coworkers (Simpson and Awapara 1966, Stokes and Awapara 1968, Chen and Awapara 1969) favour the latter interpretation, at least in some species of mollusc. They have shown that the final products of metabolism in Rangia cuneata (Gray) are alanine and succinate, under aerobic as well as anaerobic conditions. Thus the 'normal' glycolysis and Krebs cycle system is not operating in this species. Freedman (1975) discusses the fact that oysters have an unusual Krebs cycle system. It is possible that many molluscs and other organisms might be under evolutionary pressure to develop and maintain a metabolism capable of efficient utilization of food substances under relatively

anaerobic conditions (Newell 1964, Macan 1974). McLusky (1969,71) discusses the low oxygen concentrations which can occur in estuarine mud such as that inhabited by P. jenkinsi and the other brackish water Hydrobiidae. Awapara and Simpson (1967) state that there is no concrete evidence for the universality of the Krebs cycle as determined in vertebrate species. This has some interesting consequences for molluscan environmental physiology. Hochachka (1967) states that low temperatures favour anaerobic glycolysis in trout muscle. This is conceivable for molluscs also, especially in the light of Awaparas work. If a mollusc exhibits an exploitive approach to temperature conditions it will become quiescent at low temperatures and will metabolize basally. Tribe and Bowler (1968) and Newell (1964) note the possibility that intertidal molluscs could have facultatively anaerobic metabolic pathways. McMahon (1975) states that Laevapex fuscus, a frehwater limpet, can use its carbohydrate stores 'anaerobically in the extremely low oxygen tensions that can be encountered by overwintering populations'.

The importance of amino acids and specifically alanine as an endproduct of anaerobic metabolism is significant considering the role of amino acids in the type of osmotic control used by invertebrates (see Gilles 1975). Thus we have a metabolic explanation of how molluscs could provide themselves with the necesary quantities of osmotically active amino acids even under adverse conditions of low oxygen.

Thus since it is known that P. jenkinsi uses oxygen (Lumbye 1958, Heywood and Edwards 1962, Lumbye and Lumbye 1965, Duncan 1966) and hence some type of 'Krebs' cycle in oxidative metabolism, it seems likely that temperature - salinity interactions at the biochemical level will involve the switching of metabolites into various channels around this. If Hochachka's scheme derived from work on trout muscle is applicable to molluscs, less carbon will enter their citric acid pathways as temperature

falls. This would have a marked effect on (1) the amount of carbon available for the production of amino acids and (2) the availability of energy for all physiological processes including osmotic control (at low temperatures poikilotherms are less active and need less energy). The specific nature and importance of such changes is unclear. Further, cell permeability itself undergoes compensation for temperature. The tendency towards increased leakiness at high temperatures is controlled by changesin membrane composition (Hazel 1973).

Thus the ability of organisms to withstand certain osmotic conditions will be significantly altered by temperature which has a profound effect on all aspects of metabolism and more importantly those which are of special concern to osmotic and ionic regulation (see Rao 1967 for a general scheme). Klekowski and Duncan (1966) have shown that at high^{temps} *P. jenkinsi* survive better at elevated salinities, presumably due to a decrease in osmotic stress or some ionic effect stabilizing metabolism.

Environmental variables affect enzyme activity and stability (Hochachka and Somero 1973). As has been stated this can have profound effects especially if it occurs at branch points in metabolism. Narasimhan and Krishnamoorthy (1975) have shown that levels of muscle polysaccaride decrease significantly with increased adaptation salinity in a species of euryhaline crab. Thus salinity, as well as temperature, can have effects on the partitioning of carbohydrate for various activities. Krishnamoorthy and Venkatramiah (1971) have shown that both the Km and V max of myosin ATP ase are affected by salinity adaptation. These enzyme parameters are also affected by temperature. The same authors in their 1969 paper showed that this enzyme was qualitatively different in animals adapted to different salinities. Thus as in response to temperature, organisms can synthesise suitable for certain salinity conditions. It was shown that

this particular high salinity myosin ATP ase was comparatively thermo and pH stable. The authors conclude that since these crabs (Scylla serrata) experience simultaneous changes in salinity and temperature the same compensatory macromolecular mechanism is involved in compensation for both. Thus the mechanism of salinity adaptation is a corollary of that for thermal adaptation.

Organisms respond to environmental change by (amongst other things) altering their enzymes to suit conditions. Each type of a given enzyme will be most suitable only under certain sets of conditions. Thus there will be high and low temperature isoenzymes but these may be high and low salinity or pH enzymes also. The organisms primary problem would seem to be integration and coordination of response in choosing the most suitable compromise enzyme for a set of conditions. The organisms ecological and evolutionary problem should be simplified by the likelyhood that not all combinations (Hi Lo) of all the variables are possible in the species niche.Further, it is reasonable to expect that adverse combinations of factors will define species limits as will absolute levels of some factors if they sufficiently dominate the situation. The effect of any single factor will depend on the levels of a number of other physical, chemical and biotic variables. It seems likely that estuaries will demand greater enzyme flexibility of an animal since there is a constant multi - factor flux of conditions at any single locality. Freshwater and marine environments are relatively constant at a given place. Fretter and Graham (1962) in discussing the salinity tolerance of H. ulvae, H. ventrosa and P. jenkinsi state that 'a combination of features regulates their distribution and not salinity alone'.

The interactive effects of different environmental variables at the single enzyme level provide a mechanism for synergism. For instance, if a given enzyme will respond possitvely to certain separate changes in

temperature and salinity there is no reason to suppose that its response to the same changes in both factors at once should simply be additive. Further, since both factors may be affecting the activity of 'key' enzymes at branch points in metabolism powerful possibilities for synergism exist. This work has provided evidence of synergistic effects on growth but the causes are still a matter for conjecture. However, the mechanisms proposed provide a reasonable working explanation consistent with current thinking on biochemical adaptation (see Freedman 1975).

It would appear that organisms have evolved a unified approach to environmental change, at the enzyme level. Qualitative and quantitative changes in enzyme levels affecting their activation energies and affinity for substrate will adjust metabolism to the new conditions. The changes, as Rao (1967) has shown for temperature, may be very complex. As Hochachka (1967) shows, the genotype of the cells is strongly involved. Gene expression varies with conditions.

Clearly, the genotype of the cells under consideration and the expression of that genotype in the phenotype will have a marked effect on their responses. Cells from different tissues in the same organism and from corresponding tissues in different species or individuals with different environmental histories, may behave differently. Hochachka (1967) has shown that trout liver and muscle behave differently in response to low temperature acclimation. It was also demonstrated that different species of fish had different numbers of lactate dehydrogenase isoenzymes available for metabolic control.

Thus, since genetic control of response to environmental perturbations is of paramount importance, the evolutionary background of the species will set its limits of tolerance and levels of activity. The physiological activities of different species evolved for life in different ecological niches will be affected differently by combinations

of environmental variables. Thus survival in different conditions of temperature and salinity may be maximised by ; low/low, low/high, high/low or high/high combinations (Kinne 1964).

Insufficient information is available for the formulation of universally applicable models of physiological response to environmental change (see Gilles 1975a on temperature). Predictions of physiological performance in multi - variable habitats are difficult. P. jenkinsi and many other species show different optimal responses to conditions for different physiological processes. Freshwater species also have euryplastic phenotypes enabling them to survive under a wide range of conditions. This exposes them to different combinations of factors (because many of them are tolerant of wide ranges of a number of factors), at least some of which may cause synergistic responses.

4.6. Growth Control and General Theory

Some allusion has been made in this thesis to the growth equation of von Bertalanffy. This equation has been criticized both because the values of the parameters,as empirically determined,do not conform to the theory (Hemmingsen 1960) and as a result of philosophical and theoretical considerations(Taylor 1960, Hubbell 1971, Calow 1973). Calow and Hubbell criticize Bertalanffy's work because of its 'reductionist' basis. Growth is seen as a simple result of the difference between anabolism and catabolism, whilst the 'Holist' view is that control is of the essence : animals are goal directed and growth is seen as a flexible but programmed process.

Calow (1973) demonstrates the use of both a 'reductionist' and a 'holist' approach to the growth of Planorbis contortus (Linn.). A 'reductionist' model fits the data for the growth response to temperature whilst a holist model is applicable to the controlled response to food deprivation. Both P. contortus and P. jenkinsi exhibit temperature dependent growth. Fig 17 demonstrates the absence of control (see Calow 1973 for P. contortus) whilst Figs 15 and 16 show that the Arrhenius model fits the data. This implies that the temperature effect on growth, in P. jenkinsi , may be explained in terms of simple stimulation of metabolism due to changes in the available kinetic energy. The growth biochemistry of the species is not adapted to modulate the effect of temperature and so the growth rate responds in a relatively simple manner to the environmental 'input'.

The growth response of P. jenkinsi to changes in salinity is of an entirely different nature to that for temperature. The species controls its growth with respect to changes in environmental salinity in much the same way as P. contortus exerts growth regulation in the face of food withdrawal (Calow 1973). If food is only available to P. contortus for

a proportion of the time the animals feed more actively when it is present. This enables them to maintain a growth rate which tends towards that exhibited when food is constantly available. Their growth rate is not proportional to the percentage of the time when food is available. Similarly, the growth of P. jenkinsi does not decrease proportionately with a decrease of salinity from the optimum. Figs 18-22 demonstrate the control of growth rate by P. jenkinsi maintained under different salinity regimes. Thus the effects of temperature and salinity on the growth of P. jenkinsi are qualitatively different, due to the intervention of a control apparatus for the latter.

These differences in response lead to the question : why is the growth of snails controlled with respect to food availability (P.contortus) and salinity (P.jenkinsi) when it is not regulated in the face of temperature variation ? It is not that the effects of temperature are fundementally uncontrollable. Biological clocks and basal metabolism show temperature independence in some organisms (Newell 1973, Lewin 1975). It seems reasoable that the type of response an organism makes to an environmental variable will be a direct reflection of the evolutionary interaction between it and the species. Evolutionary and ecological success will be enhanced by the optimal use of and adaptation to, the environment. Since the habitat is made up of a host of qualitatively different factors, varying in many different spatial and temporal ways, it would be expected that some variation in the type of response to these should exist.

Temperature is more pervasive than salinity. By definition small poikilotherms such as P. jenkinsi do not control their body temperature and so their most fundamental levels of organisation (sub-cellular, biochemical) are exposed to the full range of environmental variation. These mechanisms are however protected from unfavourable ionic and osmotic effects (Bryan 1963, Todd 1964, Duncan 1966). It is well known that cells generally maintain a different and more controlled ionic regimen than the blood.

Thus the growth response to temperature will depend on effects at the molecular level whilst that to salinity will presumably reflect the nature of the mechanisms controlling internal ionic conditions. As Dixon and Webb have shown enzymic effects are also possible as a result of salinity change (see Gilles 1975 also). An animals enzymes will therefore respond to the residual salinity change (internal) allowed by the blood and cellular ionic and osmotic regulatory mechanisms.

Mechanisms by which poikilotherms could control their growth in response to temperature changes have been discussed (sections 4.5.3. and 4.5.6.) . It appears that P. jenkinsi has adopted an exploitive stance making use of high temperatures to promote growth. The species ecology is apparently organised such that it can survive having a low growth rate in the cold winter period. Since the species can exert no physiological control it must rely on correct evolutionary adjustment of its growth response to the environment.

The control of growth (and presumably reproduction etc.) with respect to salinity facilitates the wide range of tolerance and distribution of the species in estuarine and fresh water.

4.7. Conclusions : The Ecological Significance of the Study

It has been shown that P. jenkinsi survives in water ranging from 0 to 28°/oo salinity and 5 to 30°C. Some growth occured at all the tested combinations of these (growth expt 4). Growth was stimulated in the mid - range of salinity and as the temperature approached 25°C.

No attempt was made to define the absolute limits of salinity and temperature for growth since such results are , in an ecological context, quite meaningless. Growth will cease between 0 and 5°C and the animals tend to die at about 35°C. P. jenkinsi does not naturally experience salinities outside of the range 0 - 28°/oo. If it is required to explain ecological results in terms of environmental effects on physiological performance the limiting levels will not be where a total cessation of operation occurs . The results of this work indicate that P. jenkinsi will maintain a viable population in freshwater where the temperature reaches or exceeds (within reason) 10°C over the summer period. Given that some slow growth occurs over the winter period there is sufficient time for the animals to reach reproductive maturity (see Table 12 - section 3.4.). In estuarine conditions of elevated salinity where growth is accelerated, a shorter and or cooler summer might be tolerated in the absence of other depressant factors.

The results of this growth study give predictive information of a relative nature. Thus,other things being equal, growth will be faster in nature at 15 than 10°C or at 7 rather than 0°/oo salinity (etc.). Absolute levels of growth activity in the field cannot be predicted. The natural habitats occupied by P. jenkinsi vary qualitatively and quantitatively due to differences in a large number of both biotic and abiotic factors. Hubendick (1958) cites the following environmental variables which are of importance to freshwater molluscs : size, volume& depth of water body; shore profile, water movement, temperature, changes in water level, insolation,

transparency, suspended matter, pollution, substratum, vegetation, dissolved gasses, dissolved minerals including salinity, pH, other organisms and population characteristics (inter and intraspecific interactions). Kinne (1960) assumes that only a few master factors are of importance in defining a given ecological situation. This may be so in a gross sense but since there is a distinct lack of well defined multifactorial experimentation it is hard to see how the assertion that only temperature, salinity, light, depth and substratum are of major importance, is justified. In some environments the effects of specific factors are relatively unknown. For instance, McLusky (1969) notes a lack of knowledge concerning the effects of pH on estuarine life.

Clearly some factors are more important than others but it seems reasonable that organisms should be sensitive and responsive in some degree to all variation since they must maintain a highly specific and controlled internal regimen which must interact with the environment. Individually less important factors may exert considerable modulating influence on the effects of other more important variables. This may be of especial significance when conditions due to the 'master factors' render the existence of the individual or population marginal. This work has demonstrated the synergistic effects of temperature and salinity on the growth of P. jenkinsi. The degree of synergism varies with the particular combination of these environmental variables. Seasonal changes in the degree of synergism are therefore likely. Such interactions may not be restricted to salinity and temperature.

There are further problems associated with the prediction and comparison of ecological performance in fresh water and estuarine organisms such as P. jenkinsi. Natural habitats are subject to varying degrees of fluctuation of physical and chemical characteristics. The differences between habitats may be complex and subtle. Comparing,

predicting and evaluating component effects under such conditions is very complex. The animals in the growth experiments presented in this work were living under a qualitatively different temperature regime to that found in nature and especially in estuaries (lab. work const. temp., nature fluctuating). Odum (1971) states that 'Temperature variability is extremely important ecologically. A temperature fluctuating between 10 and 20°C and averaging 15°C does not necesarily have the same effect on organisms as a constant temperature of 15°C. It has been found that organisms which are normally subjected to variable temperatures in nature (as in most temperate regions) tend to be depressed, inhibited or slowed down by constant temperature'. Thus it is likely that the laboratory results underestimate the growth of P. jenkinsi in nature. Presumably this does not affect their general comparative value.

P. jenkinsi has a variable high salinity limit in different estuaries and fjords (Ellis 1932, Fretter and Graham 1962). Muus states that the species may be numerous and dominating up to about 7°/oo salinity and 'sporadic' up to salinities fluctuating between 20 and 24°/oo. There are a number of possible explanations for this. Either the animals are endogenously variable and physiological races exist at different localities or other environmental factors are responsible for modifying the response of the species. Fretter and Graham (1962) state that 'field and experimental results indicate that in the Hydrobiidae a combination of features regulates their distribution and not salinity alone.'

These differences in distribution may be due to different combinations of water quality, temperature and substrata etc. However, competition may also occur in waters of elevated salinity. Muus (1967) observes that P. jenkinsi H. ulvae and H. ventrosa are never all numerous at the same locality whilst H. neglecta can occur sympatrically with either of the latter in large numbers. Since very dense populations of these

molluscs occur (up to about 50,000 /m^2) it is possible that P. jenkinsi may be excluded from higher salinities by these other members of the Hydrobiidae which are presumably better adapted to them (Muus 1967).

Thus the study of environmental physiology in the field and especially in fresh water is fraught with difficulties particularly when dealing with an animal such as P. jenkinsi where the genetic structure of the population is unknown but the existence of races is suspected. This laboratory study has defined the growth response of a homogenous population of P. jenkinsi to salinity and temperature. It is proposed that the responses shown probably represent the growth potential of P. jenkinsi in Britain, or at least that of those conforming to Warwick's strain A, if racial division can be successfully demonstrated.

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5. Summary

1) The growth of P. jenkinsi has been characterised with respect to salinity and temperature. The optimum conditions for growth are 25°C and 14°/oo salinity. Synergistic effects of combinations of salinity and temperature have been observed.

2) The allometric relations between shell length and organic carbon content have been quantified under a large range of combinations of salinity and temperature. The expression for this relation is of the form :

$$c = A\, l^{m} \quad (1)$$

where c-organic carbon, l-shell length, a&m-constants.

This may be expressed in a linear form :

$$\log c = m \log l + a \qquad (\text{where } a = \log A \text{ - eqn. 1})$$

This equation is employed in comparisons of the relationship between animals grown under different conditions and for the conversion of growth rate results in terms of shell length to carbon based terms.

3) The organic carbon content of P. jenkinsi has been found to be linearly related to total dry weight. The slope coeficient n (where $c = n\, w + b$) shows temperature related trends.

4) The variation in growth rate with conditions was examined using both length and carbon based terms. Carbon has the advantage that it is interspecifically comparable. However, it is a destructive method and cannot be used, as length can, for repeated measurements on the growth of an individual animal : it must be related to such measurements by regression. The method of carbon analysis employed has proved to be sensitive and accurate.

5) Growth is controlled in relation to salinity but the response to temperature conforms to the Arrhenius model, there being no apparent regulation.

6) There appears to be some seasonal variation in growth potential in P. jenkinsi.

7) This work supports the view that P. jenkinsi is both eurythermal and eurysaline.

8) This work confirms the view of Kinne (1960) that it is combinations of environmental factors that are of importance to the survival and activity of organisms.

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APPENDIX I

ON THE EXISTENCE OF DISCRETE MORPHOLOGICAL TYPES WITHIN THE SPECIES POTAMOPYRGUS JENKINSI (SMITH)

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(Paper accepted for publication in the 'Proceedings of the Malacological Society of London')

Introduction

The work presented here was done in preparation for growth studies, on Potamopyrgus jenkinsi (Smith), by the author. It was thought necesary to take some account of the current dispute about the possible existence of subgroups within the species and produce some evidence which would indicate whether such strains exist, and whether they are of practical importance in physiological experiments.

The species has been described as consisting of three genetic strains (Warwick 1952,69). This work is of a descriptive and qualitative nature and the distinguishing factors are susceptable to subjective interpretation. The distinctness of the strains has recently been questioned (Winterbourn 1972) and some quantitative evidence was presented in support of the view that there is continuous variation between the extremes represented by Warwick's types A, B and C. Winterbourn states that the shell forms and pigmentation characteristics of 'the two main strains intergrade and strain B individuals appear to represent one phenotypic extreme in a variable series'.

The experiments presented here were performed on a scale large enough to justify the use of statistical analysis in order to provide an objective view of the state of the species.

Warwick's strain A is the most common of the three in Europe. The shell is comparatively slender with shallow sutures and somewhat flattened

whorls. The mantle colour is paler than is found in strain B (P. jenkinsi sensu stricto : Warwick). The pigment spot behind the eye is less marked.

Strain B is relatively stout with more covex whorls and deeper sutures. Strain A never exhibits the dark mantle pigmentation shown by this type.

Strain C is described as having a shell shape similar to that of strain B 'with slender and stout forms occuring'. This is somewhat ambiguous but evidence presented here suggests that C tends to be intermediate between A and B with somewhat more affinity for A. Type C exhibits mottled mantle pigmentation which develops with age (Personal communication - T. Warwick).

P. jenkinsi with keeled shells are most likely to be strain C as a high proportion of these are ornamented. Types A and B are much less commonly keeled. Type C animals, some of them keeled, have been found coexisting with strains A and B at Inchira on the River Tay.

It has been proposed that the distribution of the strains are different. This, in conjunction with the differences in morphology, possible differences in osmotic behaviour (Todd 1964), and his as yet unpublished work, are thought by Warwick to constitute grounds for reclassification of the strains as separate species.

Methods

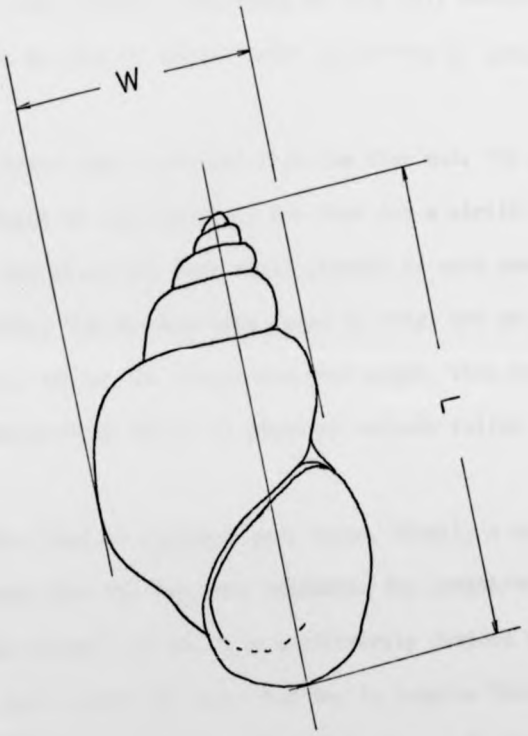
The work presented is methodologically simple. A straight - foreward analysis of shell length/width ratios was performed. This ratio may be simply related to a subjective assessment of slenderness or stoutness and hence to Warwick's classification of the animals into strains.

A dissecting microscope was used at x20 magnification with a calibrated graticule. Length and width were measured to the nearest 0,05mm.

Figure 26

Drawing of P. jenkinsi showing the measurement of length and width.

easurement of



with the animal viewed as in Fig 26.

Animals of known and unknown strain were used. All identification was done by T. Warwick. A range of sizes of animal were used in order to elucidate any developmental changes in shell morphology.

As stated, types A, B and C coexist at Inchira on the River Tay. The habitat is a tidal mudbank consisting of fine silt containing much detritus. There is also an area of stones under which many P. jenkinsi may be found.

Many animals were extracted from the fine mud. The substrate was placed in trays to a depth of approximately one inch and a similar depth of water was poured over and mixes in. Some small plastic or card sheets were placed vertically in this. The animals were found to crawl out on to these and the container walls, whilst the mudsettled over night. This has been found to work quite efficiently where all physical methods failed to effect a separation.

Two main lines of approach were tried. Firstly a very large random sample of animals from the Tay were measured. The length/width ratio was determined for each animal and the data arbritrarily divided into three size ranges 0 - 1.99, 2.0 - 2.99 and 3.0 - 4.0 mm. in length. This was done in order to exclude the possibility that developmental changes in the L/W ratio might obscure any variation, between animals of the same size, attributable to the presence of different strains. The results are shown in Fig 27.

The second part of the work was performed on animals of known strain including type A animals from the River Ore ; a freshwater stream. The length/width data from this work have been treated in two ways. The samples were more homogenous than in the random sample experiment and hence some distributions were produced using all the animals of each strain. These are shown in Fig 28. The data was also subdivided so that direct comparisons

Figure 27

The frequency distribution of the length/width ratios of three size ranges of randomly selected P. jenkinsi from the River Tay. These samples contain animals from all three strains.

° less than 2.0mm.

• 2.0 - 2.99mm.

▪ greater than 3.0mm.

Figure 27

The frequency distribution of the length/width ratios of three size ranges of randomly selected P. jenkinsi from the River Tay. These samples contain animals from all three strains.

° less than 2.0mm.

• 2.0 - 2.99mm.

▪ greater than 3.0mm.

ngth/width ratios

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trains.

Figure 28

The frequency distributions of the length/width ratios of the three different strains of P. jenkinsi.

▪ strain A

▫ strain B

• strain C

ength/width ratios

could be made between animals of similar length.

Results

The distribution of the L/W data from the large samples of unidentified animals do not show any clear bi or trimodality (Table 19 and Fig 27). It appears that from a population proposed to be a mixture of three well represented strains there is a continuous broad spread of L/W. Even if the strians do exist there appears to be a considerable morphological overlap. The range of L/W ratios within the species is high even within the size ranges shown. The population is certainly highly variable with respect to shell morphology.

The interpretation of the results from the work on identified animals is more difficult. An analysis of variance between all of the animals in the three groups A, B and C (River Tay) (see Tables 21 and 22) gives an F ratio of 35.3 which is significant at the 0.1 % level. The samples of A and C are shown by t tests to be significantly different from B (o.1 %). However, A and C are only just significantly different at a reduced confidence level (1%) (Fig 28).

The data from the River Ore animals (Table 20) was included in a second analysis of variance with the Tay data. The F ratio was 31.8 : significant at the 0.1 % level. River Ore snails were compared to those from the Tay by t test. Ore A types are significantly different (0.1 %) from both Tay A's and B's. They are also different from Tay C's but only at 1 %. This result does not increase confidence in the existence of the strains but may indicate some pleitropic effect (see Table 22).

In order to clarify the situation further the data was sub - divided into the length ranges 1.5 - 1.99, 2.5 - 2.99, 3.0 - 3.49 and 3.5 - 4.0 mm. in which statistically significant numbers of measurements were

present. Within each strain analysis of variance between the size range sets demonstrates a developmental change in L/W (F ratio sig. at 0.1 %). Table 23 shows the trend in all the strains to be towards a more slender shell as age and length increase . This justifies the subdivision of the data for the comparison of the strains, as the developmental change in L/W would otherwise obscure the differences between them. Analysis of variance within each size range, between the strains,shows that they are significantly different at the 0.1 % level except in the 3.0 - 3.49 mm. group where the confidence level is only 1.0 %.

These results are in some ways conflicting. The large random samples show continuous variation, whilst selected identified animals prove to be statistically separable. Z tests were performed on the Tay A, B and C data (Lewis 1966) to give a confidence value to the intersects of their distributions of L/W for separation of the strains on this basis alone. These predict between A and B, and C and B respectively that there are 20 and 29 % chances of error in selection between these pairs. Types A and C are even less significantly different. The chances of error will be extremely large when selecting from a sample containing all three strains. Hence for practical purposes stoutness of shell is a useless determinate for the subdivision of the species.

It is necesary to give some consideration to the validity of the attempt to describe the type of observations presented here, by'objective' statistical methods. The animals that have been grouped into strains have been identified using a subjective analysis of their morphology employing all the factors described earlier. This includes considerable reference to the factor (L/W - stoutness) for which an objective analysis is being sought. Hence the 'objective' results may be biased by preselection. In this case it is possible that preselection has tended to increase the apparent

differences between the strains. This tends to give further support to the view that no clear subdivision of the species, on the basis of shell shape alone, is possible.

Discussion

The results shown indicate that shell morphology cannot, in this case, be used to provide an objective criterion for the subdivision of the species.The other factors that have been suggested are difficult to employ and rather subjective. Physiological experiments may provide means with a higher degree of resolution but work to date indicates a high degree of individual variability. Thus it seems likely that some cytogenetic differentiation may be the only truly objective criteria.

The obvious question to ask in a situation of this type is whether there is anything to be gained by the subdivision of a previously usefull taxonomic unit. Sheppard (1967) defines the species problem in quite simple terms describing a species as a 'population or group of populations which are capable of exchanging genes, one with another in nature, if they come into contact.' Subspecies or geographical races possess distinguishing characters but are capable of hybridization. It is obvious that when considering a parthenogenetic animal such as P. jenkinsi there are definit problems in applying the terms species and race to the whole group or subgroups within the population.

It is obviously usefull to define this group of animals as a species. Subdivision would seem to be of dubious merit. Warwick's types may be defineable entities but they do not seem to be thoroughly justifiable as many individuals do not seem to fall clearly into any given group.

White (1970) has given consideration to variability and polymorphism in parthenogenetic animals and he is of the opinion that in

reality they do not exhibit the 'chaotic variation' that might have been expected. Mayr (1963) argues that a low level of variation in parthenogenetic animals is due to the non-expression of mutants most of which are recesive. This suppresive effect is even more powerful in tetraploid animals where there are three wild type alleles competing with each mutant. British P. jenkinsi are possibly tetraploid (Sanderson 1940)

White's review indicates that parthenogenetic animals generally exhibit either one or a small number of types with definit cytogenetic characteristics. Where there are a number of types it is proposed that they represent the multiple origin of parthenogenesis in that species. If this is the case then P. jenkinsi could exhibit three sets of cytogenetic variants corresponding to each of the three strains. How these would relate to the existence of diploid and tetraploid variants is not clear. A polymorphism in P. jenkinsi could be supported by a replacement of one or more morphs by another, as in industrial melanism, or by a favouring of different morphs by different habitats. Either of these possibilities is acceptable if one takes the view that P. jenkinsi has recently changed from a sexual to a parthenogenetic mode of reproduction, is a migrant from New Zealand and has newly adapted to the freshwater environment. Warwick has proposed that the strains are favoured by different habitats ; A by inland fresh water although it does frequently occur near the coast and in quite brackish water ; B by coastal water bodies (fresh and brackish) whilst C which is rare has a distribution similar to B. The strains are far from allopatric and sometimes coexist. Heterozygosity could not support polymorphism in a parthenogenetic animal as there is no recombination.

Summary

1) Subspecies of P. jenkinsi may exist but objective

analysis of subjectively preselected data whilst supporting Warwick's hypothesis is questionable in itself.

2) Distributions of very large numbers of results show continuous variation and no bi or trimodality for L/W.

3) As a result of the limitations of the physiological experiments that could reveal differences in subgroups, cytogenetic methods are the only ones which could provide objective criteria for the subdivision of the species.

4) As a conclusion it must be stated that genetic strains of P. jenkinsi may well exist. However, the animal is so highly variable as to render subdivision, on a purely morphological basis,untenable. Whilst cytogenetic studies may reveal absolute differences these cannot be employed if the material is to be kept in a living state for further experimentation. Thus it is suggested that P. jenkinsi be retained as a species unit, whilst recognising that it may be genetically heterogenous.

Table 19

The length, width and length/width ratios of individual *P. jenkinsi* randomly selected from samples collected at Inchira on the River Tay. Animals from all three strains are present.

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nt.

Length 0-2.0mm.

L		L/W
1.5	0.95	1.58
1.8	1.0	1.8
1.6	1.0	1.6
1.7	0.95	1.79
1.85	0.9	2.06
1.9	1.0	1.9
1.8	0.95	1.89
1.5	0.95	1.58
1.3	0.80	1.63
1.5	0.90	1.67
1.3	0.8	1.63
1.3	0.85	1.53
1.8	1.1	1.64
1.55	0.9	1.72
1.65	1.1	1.5
1.55	1.0	1.55
1.95	1.0	1.95
1.5	0.9	1.67
1.9	0.95	2.0
1.2	0.8	1.5
1.5	0.9	1.67
1.45	0.85	1.71
1.7	0.9	1.89
1.9	1.15	1.65
1.8	1.1	1.64
1.7	0.95	1.79
1.7	1.05	1.62
1.4	0.85	1.65
1.3	0.8	1.63
1.25	0.8	1.56
1.1	0.65	1.69
1.75	1.05	1.66

L		L/W
1.8	1.1	1.64
1.7	0.9	1.88
1.9	1.0	1.9
1.95	1.2	1.63
1.7	1.0	1.7
1.6	1.0	1.6
1.45	0.9	1.61
1.55	0.9	1.72
1.55	0.85	1.82
1.35	0.85	1.59
1.25	0.75	1.67
1.9	1.15	1.65
1.8	1.1	1.64
1.5	0.85	1.76
1.5	0.8	1.88
1.85	1.1	1.68
1.65	0.8	2.06
1.5	0.8	1.88
1.6	0.9	1.78
1.2	0.65	1.85
1.6	0.95	1.68
1.5	0.9	1.67
1.35	0.85	1.59
1.85	1.05	1.76
1.5	0.9	1.67
1.6	0.85	1.88
1.7	0.9	1.89
1.6	0.95	1.68
1.65	0.85	1.94
1.25	0.85	1.56
1.45	0.8	1.81
1.95	1.0	1.95

L		L/W
1.35	0.9	1.5
1.3	0.75	1.74
1.75	0.95	1.84
1.8	1.1	1.64
1.95	1.0	1.95
1.7	0.9	1.89
1.55	0.9	1.72
1.35	0.85	1.59
1.2	0.7	1.71
1.4	0.85	1.65
1.3	0.85	1.76
1.9	1.15	1.65
1.9	1.0	1.9
1.5	0.85	1.76
1.5	0.8	1.88
1.55	1.0	1.55
1.5	0.9	1.67
1.95	0.95	1.95
1.6	0.95	1.68
1.9	0.85	1.76
1.45	0.8	1.81
1.45	0.9	1.61
1.8	1.15	1.57
1.65	0.9	1.83
1.75	1.0	1.75
1.55	0.85	1.82
1.5	0.9	1.67
1.75	0.9	1.94
1.0	0.95	1.89
1.3	0.85	1.53
1.9	1.05	1.80

Length 2.0-2.0[illegible]

L		L/
2.5	1.5	1.67
2.0	1.0	2.0
2.3	1.3	1.77
2.7	1.4	1.93
2.6	1.2	2.17
2.2	1.1	2.0
2.0	1.0	2.0
2.1	1.2	1.75
2.0	1.0	2.00
2.7	1.25	2.16
2.0	1.05	1.9
2.6	1.3	2.0
2.0	1.0	2.0
2.15	1.1	1.95
2.0	1.45	1.93
2.4	1.3	1.84
2.4	1.6	1.5
2.85	1.65	1.72
2.1	1.3	1.61
2.35	1.25	1.88
2.3	1.4	1.64
2.4	1.45	1.65
2.1	1.35	1.55
2.2	1.25	1.76
2.1	1.2	1.75
2.75	1.45	1.89
2.7	1.5	1.8
2.55	1.45	1.75
2.75	1.55	1.77
2.9	1.6	1.81
2.3	1.4	1.64
2.25	1.35	1.66
2.05	1.3	1.57
2.2	1.25	1.76

L		L/
2.3	1.3	1.77
2.0	1.5	1.87
2.9	1.5	1.94
2.4	1.1	2.11
2.1	1.3	1.62
2.15	1.05	2.05
2.2	1.3	1.69
2.25	1.3	1.73
2.7	1.3	2.08
2.45	1.25	1.96
2.1	1.0	2.1
2.6	1.3	2.0
2.65	1.2	2.2
2.3	1.1	2.09
2.8	1.4	2.0
2.05	1.35	1.51
2.0	1.25	1.6
2.9	1.6	1.81
2.25	1.35	1.66
2.2	1.15	1.91
2.9	1.6	1.81
2.5	1.45	2.0
2.25	1.35	1.66
2.55	1.5	1.7
2.2	1.15	1.91
2.8	1.4	1.70
2.75	1.45	1.89
2.45	1.5	1.63
2.9	1.5	1.93
2.65	1.45	1.82
2.15	1.35	1.59
2.35	1.4	1.67
2.0	1.35	1.48

L		L/
2.1	1.3	1.62
2.9	1.5	1.94
2.6	1.3	2.0
2.4	1.4	1.72
2.0	1.1	1.82
2.0	1.2	1.67
2.0	1.2	1.67
2.5	1.2	2.08
2.9	1.35	2.15
2.2	1.1	2.0
2.0	1.0	2.0
2.8	1.4	2.0
2.4	1.1	2.18
2.2	1.15	1.91
2.1	1.15	1.82
2.85	1.4	1.60
2.05	1.35	1.51
2.55	1.5	1.7
2.25	1.3	1.73
2.45	1.25	1.96
2.5	1.5	1.66
2.5	1.25	2.0
2.55	1.35	1.74
2.5	1.3	1.92
2.05	1.3	1.57
2.65	1.5	1.76
2.75	1.45	1.89
2.75	1.5	1.83
2.9	1.5	1.93
2.75	1.55	1.77
2.3	1.5	1.53
2.1	1.35	1.55
2.3	1.35	1.7

Length 3.6–

L	W	L/W
3.0	1.3	2.12
3.7	1.6	2.32
3.8	1.6	2.38
3.8	1.6	2.38
3.9	1.6	2.44
3.0	1.3	2.31
3.65	1.5	2.43
3.65	1.5	2.43
3.7	1.9	1.95
3.7	1.75	2.12
4.0	1.7	2.36
3.65	1.6	2.28
3.95	1.5	2.63
3.1	1.4	2.43
3.4	1.6	2.13
3.5	1.6	2.19
3.10	1.65	1.87
3.3	1.55	2.06
3.45	1.6	2.15
3.5	1.85	1.89
3.45	1.85	1.86
3.05	1.65	1.84
3.1	1.7	1.82
3.7	1.85	2.0
3.7	1.75	2.11
3.1	1.6	1.93

L	W	L/W
3.4	1.5	2.27
3.4	1.8	1.89
4.0	1.7	2.36
3.0	1.5	2.0
3.0	1.4	2.15
3.85	1.8	2.14
3.35	1.7	1.97
3.6	1.7	2.12
4.0	1.9	2.11
3.7	1.8	2.06
3.7	1.6	2.3
3.7	1.6	2.31
3.9	1.65	2.52
3.95	1.5	2.63
3.7	1.7	2.18
3.05	1.5	2.03
3.7	1.65	2.2
3.7	1.8	2.05
3.3	1.75	1.88
3.3	1.85	1.78
3.3	1.75	1.88
3.5	1.75	2.0
3.55	1.7	2.08
3.4	1.65	2.06
3.2	1.75	1.82

L	W	L/W
3.5	1.7	2.06
3.9	1.7	2.3
3.9	1.6	2.44
4.0	1.5	2.67
3.5	1.5	2.34
4.00	1.5	2.67
3.6	1.7	2.12
3.7	1.5	2.47
3.65	1.65	2.21
3.5	1.6	2.19
3.5	1.5	2.33
3.6	1.55	2.32
3.75	1.5	2.50
3.3	1.45	2.28
3.8	1.7	2.24
3.2	1.55	2.06
3.1	1.55	2.0
3.1	1.65	1.87
3.2	1.7	1.88
3.55	1.8	1.97
3.35	1.7	1.97
3.0	1.6	1.87
3.5	1.6	2.18
3.05	1.65	1.84
3.25	1.55	2.09

Table 20

The length, width (in mm.) and length/width ratios of individual *P. jenkinsi* taken from the River Ore. Only strain A snails are present in this sample.

th/width ratios of

nly strain A snails

L	W	L/W	L	W	L/W	L	W	L/W
2.7	1.4	1.93	3.25	1.75	1.86	2.95	1.5	1.97
3.55	1.7	2.09	2.95	1.55	1.91	2.15	1.25	1.72
2.75	1.5	1.84	4.0	1.8	2.23	2.9	1.55	1.81
3.35	1.75	1.92	3.85	1.9	2.03	3.4	1.7	2.0
3.85	1.8	2.14	3.55	1.7	2.08	4.1	1.85	2.22
3.85	1.85	2.09	3.65	1.75	2.09	3.45	1.7	2.03
3.05	1.55	1.97	3.3	1.7	1.95	2.85	1.6	1.78
2.7	1.55	1.75	3.1	1.7	1.83	3.25	1.65	1.97
2.9	1.6	1.82	3.25	1.75	1.86	2.8	1.5	1.87
2.2	1.4	1.58	2.3	1.35	1.7	2.35	1.4	1.67
2.4	1.35	1.77	2.45	1.3	1.88	2.3	1.3	1.76
2.35	1.35	1.74	2.35	1.3	1.8	2.3	1.3	1.76
2.4	1.3	1.84	2.3	1.25	1.84	2.65	1.45	1.80
2.60	1.5	1.73	2.6	1.5	1.73	2.65	1.45	1.82
2.65	1.5	1.76	2.60	1.5	1.73	2.65	1.5	1.76
2.65	1.45	1.82	2.6	1.5	1.73	2.1	1.25	1.68
2.15	1.25	1.72	2.25	1.35	1.66	2.75	1.45	1.89
2.75	1.45	1.89	2.85	1.55	1.87	2.75	1.5	1.83
2.75	1.5	1.83	2.75	1.45	1.89	2.75	1.45	1.89
2.5	1.4	1.78	2.55	1.35	1.88	2.5	1.45	1.72
2.5	1.4	1.78	2.45	1.45	1.68	2.45	1.4	1.75
2.5	1.5	1.66	2.55	1.4	1.82	2.55	1.4	1.82
2.1	1.15	1.82	2.2	1.25	1.76	2.25	1.3	1.73

L	W	L/W	L	W	L/W	L	W	L/W
2.1	1.25	1.68	2.2	1.3	1.69	2.2	1.25	1.76
2.25	1.25	1.8	2.9	1.55	1.87	2.9	1.55	1.87
3.0	1.65	1.81	2.4	1.3	1.84	2.4	1.4	1.71
2.4	1.35	1.77	2.4	1.3	1.84	2.4	1.4	1.71

Table 21

The length, width (in mm.) and length/width ratios of of individual P. jenkinsi from the River Tay. These animals have been divided into size range groups. They are also separated into separate strains using morphological criteria (done by T. Warwick).

th/width ratios of
animals have been
rated into separate
arwick).

Length range 1.5–1.99 mm.

Strain A			Strain B			Strain C		
L	W	L/W	L	W	L/W	L	W	L/W
1.9	1.05	1.8	1.9	1.1	1.72	1.95	1.25	1.56
1.75	1.05	1.66	1.9	1.2	1.58	1.95	1.15	1.69
1.95	1.0	1.95	1.95	1.2	1.62	1.75	1.2	1.45
1.9	1.0	1.9	1.7	1.15	1.47	1.9	1.2	1.58
1.75	1.05	1.66	1.85	1.25	1.48			
1.8	1.05	1.71	1.9	1.25	1.52			
			1.85	1.2	1.54			
			1.75	1.1	1.59			
			1.55	1.0	1.55			
			1.8	1.2	1.5			
			1.8	1.15	1.56			
			1.7	1.1	1.54			
			1.9	1.2	1.58			
			1.95	1.2	1.62			
			1.6	1.15	1.39			
			1.75	1.15	1.52			

Length range 0–1.5

Strain A	Strain B			Strain C
-	1.3	0.85	1.52	-

Length range 2.0-2.49 mm.

Strain A			Strain B			Strain C		
L	W	L/W	L	W	L/W	L	W	L/W
2.2	1.15	1.91	2.05	1.35	1.51	2.1	1.3	1.61
2.1	1.15	1.82	2.25	1.4	1.6			
2.4	1.3	1.84	2.4	1.6	1.5			
2.15	1.15	1.86	2.0	1.25	1.60			
2.0	1.25	1.6	2.05	1.35	1.51			
2.45	1.25	1.96	2.35	1.4	1.67			
2.4	1.3	1.84	2.1	1.35	1.55			
2.1	1.2	1.75	2.45	1.45	1.68			
2.25	1.15	1.95	2.1	1.3	1.61			
2.25	1.25	1,80	2.4	1.5	1.6			
			2.25	1.5	1.5			
			2.0	1.35	1.48			
			2.0	1.25	1.6			
			2.36	1.35	1.74			
			2.1	1.3	1.61			
			2.25	1.3	1.73			
			2.0	1.25	1.6			
			2.15	1.25	1.72			
			2.2	1.35	1.62			
			2.1	1.25	1.55			
			2.1	1.3	1.61			
			2.05	1.25	1.64			

Length range 2.5-2.99 mm.

Strain A			Strain B			Strain C		
L	W	L/W	L	W	L/W	L	W	L/W
2.8	1.45	1.93	2.95	1.6	1.84	2.6	1.3	2.0
2.8	1.4	2.0	2.65	1.5	1.76	2.6	1.3	2.0
2.85	1.55	1.83	2.55	1,5	1.7	2.8	1.4	2.0
2.6	1.35	1.92				2.85	1.65	1.72
						2.9	1.6	1.81
						2.55	1.5	1.7
						2.75	1.65	1.66
						2.6	1.5	1.73

Length range 3.0-3.49 mm.

Strain A			Strain B			Strain C		
3.4	1.4	2.43	3.3	1.75	1.88	3.4	1.6	2.13
3.3	1.45	2.28	3.2	1.7	1.88	3.05	1.5	2.03
3.2	1.55	2.06	3.3	1.85	1.78	3.35	1.7	1.97
3.1	1.65	1.87	3.45	1.85	1.86	3.05	1.65	1.84
3.1	1.55	2.0	3.3	1.75	1.88	3.0	1.6	1.87
3.2	1.55	2.06	3.1	1.6	1.93	3.1	1.7	1.82
3.1	1.65	1.87	3.05	1.65	1.84	3.25	1.60	2.03
3.45	1.6	2.15				3.25	1.65	1.96
3.25	1.6	2.03						
3.2	1.5	2.13						

Length range 3.5-4.0

Strain A			Strain B			Strain C		
L	W	L/W	L	W	L/W	L	W	L/W
4.0	1.7	2.36	3.9	1.9	1.95	3.7	1.7	2.18
3.7	1.6	2.32	4.0	1.9	2.11	3.8	1.7	2.24
3.5	1.5	2.33	3.65	1.65	2.21	3.5	1.6	2.19
3.65	1.6	2.28	3.5	1.85	1.89	3.5	1.75	2.0
3.7	1.6	2.31	3.55	1.8	1.97	3.55	1.7	2.08
3.6	1.55	2.32				3.75	1.85	2.02
3.95	1.5	2.63						
3.9	1.55	2.52						
3.75	1.5	2.5						
3.95	1.5	2.63						
3.7	1.65	2.2						
3.7	1.8	2.05						

Table 22

The mean lengths (mm.), standard deviations of length, mean length/width ratios and 'population' sizes (n) of the groups of animals under comparison.

viations of length,

) of the groups of

Source & Strain	Mean length	st. dev. length	Mean L/W	n
R. Ore, Strain A	2.7	0.48	1.84	81
R. Tay, Strain A	2.9	0.72	2.04	44
R. Tay, Strain B	2.3	0.65	1.66	55
R. Tay, Strain C	2.9	0.5	1.88	27

Table 23

The mean lengths and length/width ratios of different strains of *P. jenkinsi* subdivided into size class ranges.

ratios of different

s ranges.

Size range mm.		STRAIN A	STRAIN B	STRAIN C
1.5-1.99	L	1.84	1.75	1.88
	L/W	1.78	1.5	1.57
2.0-2.49	L	2.23	2.16	-
	L/W	1.83	1.6	-
2.5-2.99	L	2.76	2.71	2.70
	L/W	1.92	1.7	1.82
3.0-3.49	L	3.23	3.32	3.25
	L/W	2.08	1.8	1.95
3.5-	L	3.75	3.72	3.63
	L/W	2.37	2.02	2.11

APPENDIX II

Table 24

The length, log length, wet weight, dry weight, organic carbon and log organic carbon values of individual P. jenkinsi from the River Ore. Data for animals grown under different conditions of salinity and temperature are shown separately.

t, dry weight,

f individual

ls grown under

re are shown

0°/oo, 5°C.

length	log length	wet wt.	dry wt.	org.c.	log c.
1.15	0.0607	0.141	0.139	10	1.0000
1.5	0.1761	0.353	0.332	24	1.3802
1.45	0.1614	0.287	0.269	26	1.4150
1.9	0.2788	0.784	0.504	50	1.6990
1.3	0.1139	0.326	0.233	20	1.3010
2.05	0.3118	0.962	0.592	58	1.7634
1.8	0.2553		0.392	44	1.6435
2.2	0.3424		0.673	73.5	1.8663
1.65	0.2175		0.337	40	1.6021
1.6	0.2041		0.317	36	1.5563
2.35	0.3711		0.662	88.5	1.9469
1.5	0.1761		0.260	25	1.3979
1.9	0.2788		0.443	49	1.6902

0°/oo, 10°C.

2.05	0.312	59.5	1.7750
2.35	0.3711	55	1.7400
1.4	0.146	23.5	1.3710
1.05	0.021	7.0	0.8450
2.5	0.398	66.5	1.8228
1.0	0.0	11.5	1.0600
1.95	0.29	74	1.8690
1.5	0.19	22	1.3420
1.0	0.0	15	1.1760
1.45	0.16	19	1.2790
2.05	0.312	30	1.4770
1.45	0.161	21.5	1.3320
2.1	0.322	52	1.7160
1.0	0.0	10	1.0000
2.5	0.398	69	1.8390
2.4	0.38	42	1.623
2.25	0.352	41.5	1.618
1.7	0.243	16.5	1.218
1.45	0.161	18	1.255

length	log length	wet wt.	dry wt.	org.c.	log c.
1.4	0.146			10	1.0000
2.15	0.3324			43	1.6335
1.85	0.2672			29	1.462
2.2	0.342			35	1.544
2.3	0.362			56	1.748
2.4	0.38			35	1.544
2.25	0.352			42	1.6232
2.0	0.301			34.5	1.538
2.25	0.352			23	1.362
4.5	0.653	8.33	4.28	560	2.748
4.6	0.663	7.66	3.37	490	2.690
4.5	0.653	7.77	3.69	390	2.591
3.9	0.591	5.67	2.52	270	2.431
3.65	0.562	4.33	1.94	245	2.389
1.7	0.230			29	1.462
1.85	0.267			49	1.690
1.5	0.176	0.343	0.309	20	1.301
1.75	0.243	0.433	0.391	25	1.3979
1.4	0.146	0.379	0.275	21.5	1.332
1.15	0.061	0.222	0.195	17	1.230
1.65	0.218	0.570	0.370	32	1.5051
1.15	0.061	0.186	0.154	7.5	0.875
2.15	0.332		0.616	46	1.663
2.4	0.380		0.843	70.5	1.848
2.3	0.362		0.74	63.5	1.803
3.05	0.484		1.37	115.5	2.0607
2.4	0.389		0.908	72	2.8573
4.1	0.6128	6.02	2.67	254	2.4048
3.1	0.4914	2.48	1.35	133	2.1239
3.65	0.5623	3.83	1.79	207	2.3160
4.6	0.6628	6.61	3.05	335	2.5250
3.35	0.525	3.8	1.8	240	2.3802
4.15	0.618	5.52	2.17	260	2.415
3.15	0.4983	2.84	1.51	165	2.2175
3.5	0.5502	4.11	1.82	168	2.2253

0°/oo, 10°C cont.

length	log length	wet wt.	dry wt.	org.c.	log c.
3.7	0.5682	4.75	1.91	187	2.2718
3.35	0.5250	3.46	1.58	155	2.1903

0°/oo, 15°C

1.6	0.2041	0.56	0.302	17	1.2304
1.5	0.1761	0.505	0.289	26	1.4150
1.5	0.1761	0.514	0.291	23	1.3617
2.45	0.3892	1.46	0.820	69	1.8388
2.3	0.3617	1.2	0.756	67.5	1.8293
2.0	0.3010	0.853	0.557	43	1.6335
3.75	0.5740	4.64	1.88	180	2.2553
3.95	0.5966	5.27	2.72	187	2.2718
3.95	0.5966	5.45	2.07	207	2.3160
4.45	0.6484	7.62	3.14	300	2.4771
3.75	0.5740	4.38	1.67	190	2.2788
3.05	0.4843	2.60	1.13	122	2.0864
4.0	0.6021	5.61	2.19	258	2.4116
4.25	0.6284	5.28	2.34	216	2.3345

0°/oo, 25°C

1.25	0.0969	0.282	0.16	7	0.8451
1.3	0.1139	0.317	0.20	7	0.8451
1.75	0.2430			27	1.4314
1.7	0.2304			31.5	1.4983
1.35	0.1303	0.273	0.20	13	1.1139
4.3	0.6335	6.87	2.50	260	2.4150
4.5	0.6532	7.02	2.60	232	2.3655
3.7	0.5682	4.87	1.98	210	2.3222
3.95	0.5966	5.66	2.23	220	2.3424
4.45	0.6485	6.58	2.41	260	2.4150
3.7	0.5682	4.02	1.68	222	2.3464
2.55	0.4065	2.98	1.0	125	2.0969
2.6	0.4232	1.76	0.89	103	2.0128

0°/oo, 25°C cont.

length	log length	wet wt.	dry wt.	org c.	log c.
2.0	0.3010	1.11	0.62	90	1.9542
1.5	0.1761	0.507	0.291	26	1.4150
1.3	0.1139	0.370	0.20	19.5	1.2900
1.35	0.1303	0.254	0.195	19.5	1.2900

0°/oo, 30°C

1.35	0.1303	0.366	0.20	30	1.4771
1.4	0.1461	0.436	0.236	30	1.4771
3.1	0.4915	3.46	1.30	130	2.1139
3.5	0.5441	4.22	1.51	158	2.1987
2.85	0.4548	2.71	1.04	110	2.0414
3.25	0.5119	3.64	1.24	103	2.0128
2.6	0.4150	2.3	0.88	94	1.9731
1.6	0.2041	1.45	0.636	57	1.7559
3.3	0.5185	3.5	1.22	100	2.0000
2.4	0.3802	1.83	0.77	64	1.8062
2.75	0.4393	2.53	1.98	78	1.8921
1.5	0.1761	0.449	0.291	22	1.3424
1.5	0.1761	0.443	0.286	20	1.3010
1.0	0.0000	0.154	0.111	9	0.9542
1.5	0.1761	0.532	0.291	35	1.5441
1.35	0.1303	0.316	0.178	19	1.2788

3.5°/oo, 10°C

2.1	0.3222	1.12	0.632	66	1.8195
2.25	0.3522	1.11	0.642	80	1.9031
1.55	0.1903	0.54	0.332	38	1.5798
4.5	0.6532	7.56	3.17	380	2.5798
3.5	0.5441	4.42	2.37	270	2.4314
4.5	0.6532	7.34	3.32	435	2.6385
4.55	0.6580	7.47	3.08	410	2.6128
1.5	0.1761			32	1.5051
1.6	0.2041			37	1.5682

3.5°/oo, 15°C

length	log length	wet wt.	dry wt.	org.c.	log c.
4.85	0.6857	9.43	3.53	400	2.6021
4.9	0.6902	9.3	3.72	440	2.6435
4.85	0.6857	10.0	3.93	385	2.5855
4.65	0.6675	8.92	3.46	426	2.6294
4.75	0.6767	8.76	3.12	500	2.6990
4.75	0.6767	9.56	3.94	460	2.6628
2.0	0.3010	1.12	0.60	60	1.7782
1.75	0.2430	0.94	0.528	59	1.7709
1.8	0.2553	0.75	0.432	55	1.7404
3.9	0.5911	5.97	2.64	252	2.4014
4.25	0.6284	6.50	2.53	315	2.4983
1.3	0.1139			20	1.3010
1.4	0.1461			25	1.3979

3.5°/oo, 25°C

2.35	0.3711	1.57	0.777	60	1.7782
1.9	0.2788	0.79	0.485	45	1.6532
1.5	0.1761	0.44	0.303	28.5	1.4548
5.6	0.7482	13.7	5.43	600	2.7782
5.15	0.7118	10.8	4.33	375	2.5740
5.3	0.7243	12.8	5.03	475	2.6767
5.2	0.7160	11.3	4.24	485	2.6875
4.95	0.6946	9.1	3.8	480	2.6812
5.15	0.7118	11.8	4.82	480	2.6812
4.2	0.6232	9.2	3.97	350	2.5441
5.25	0.7202	13.0	5.09	515	2.7118
5.15	0.7118	12.2	4.59	385	2.5855
5.0	0.6990	11.1	4.72	428	2.6314
2.3	0.3617	1.19	0.763	94	1.9731
2.25	0.3522	1.15	0.765	95.5	1.9800
2.0	0.3010	0.81	0.50	56.5	1.7520
1.55	0.1903	0.395	0.30	36.5	1.5623

3.5°/oo, 30°C

length	log length	wet wt.	dry wt.	org c.	log c.
1.65	0.2175	0.70	0.397	41	1.6128
1.45	0.1614	0.31	0.226	17.5	1.2430
1.25	0.0969	0.16	0.160	9.5	0.9777
1.65	0.2175	0.460	0.359	53.5	1.7284
1.60	0.2014	0.403	0.333	52	1.7160
3.0	0.4771	2.64	1.23	130	2.1139
3.35	0.5250	3.96	1.72	112	2.0492
3.3	0.5185	3.52	1.53	100	2.0000
2.65	0.4232	1.96	1.11	97	1.9868

7°/oo, 5°C

1.35	0.1303	0.230	0.216	17	1.2304
1.5	0.1761	0.391	0.316	26	1.4150
1.2	0.0792	0.203	0.201	12	1.0792
1.0	0.0000	0.241	0.163	14	1.1461
1.75	0.2430	0.597	0.403	45.5	1.6580
1.5	0.1761	0.495	0.326	36	1.5563
2.05	0.3118	0.993	0.576	58.5	1.7672
1.65	0.2175		0.356	47	1.6721
1.5	0.1761		0.281	37	1.5682
1.5	0.1761		0.276	36.5	1.5623
2.15	0.3324		0.635	87	1.9395
1.55	0.1903		0.304	44	1.6435
2.55	0.4065		1.02	126	2.1004
2.05	0.3118		0.568	77	1.8865

7°/oo, 10°C

length	log length	wet wt.	dry wt.	org c.	log c.
1.15	0.0607			10.5	1.0212
1.4	0.1461			22	1.3424
1.5	0.1761			36.5	1.5623
1.25	0.0969			14	1.1461
1.65	0.2175			35	1.5441
1.3	0.1139	0.372	0.203	19.5	1.2900
1.05	0.0212	0.218	0.126	8	0.9031
1.35	0.1303	0.374	0.218	19	1.2788
1.05	0.0212	0.219	0.129	11	1.0414
1.9	0.2788		0.555	39	1.5911
2.2	0.3424		0.820	66	1.8195
2.95	0.4698		1.55	108	2.0334
1.7	0.2304		0.380	39	1.5911
2.4	0.3802		1.1	69	1.8388
2.6	0.4150		1.08	81	1.9085
1.85	0.2672		0.492	47.5	1.6767
1.65	0.2175		0.389	32	1.5051
4.1	0.6138	5.44	2.73	316	2.4997
4.25	0.6284	6.47	2.94	330	2.5185
4.5	0.6532	7.17	3.02	405	2.6075
4.35	0.6385	6.63	2.81	324	2.5105
4.05	0.6075	4.79	2.15	280	2.4472
4.3	0.6335	6.27	2.66	290	2.4624
4.45	0.6484	7.31	2.81	324	2.5105
3.9	0.5911	5.08	2.02	240	2.3802
4.3	0.6335	6.37	2.43	277	2.4425

7°/oo, 15°C

length	log length	wet wt.	dry wt.	org.c.	log c.
1.4	0.1461	0.465	0.30	25.5	1.4065
1.6	0.2041	0.594	0.317	27.5	1.4393
1.2	0.0792	0.280	0.179	22	1.3424
1.45	0.1614	0.417	0.233	22	1.3424
1.0	0.0000	0.156	0.116	9.0	0.9542
2.1	0.3222	1.18	0.751	65	1.8129
1.5	0.1761	0.50	0.328	39	1.5911
2.35	0.3711	1.7	0.935	81	1.9085
3.15	0.4983	2.78	1.29	160	2.2041
3.7	0.5682	3.87	1.56	195	2.2900
3.25	0.5119	2.68	1.26	160	2.2041
3.8	0.5798	4.40	1.96	210	2.3222
3.95	0.5966	4.73	2.16	250	2.3979
4.35	0.6385	7.55	2.95	282	2.4502
4.3	0.6335	7.13	2.67	258	2.4116
5.1	0.7076	11.1	4.4	500	2.6990
4.75	0.6767	9.12	3.43	332	2.5211
4.8	0.6812	9.19	3.0	280	2.4472
4.75	0.6767	9.90	3.62	335	2.5250
4.7	0.6721	9.0	3.26	315	2.4983
4.9	0.6902	10.2	3.47	337	2.5276

7°/oo, 25°C

1.35	0.1303	0.367	0.232	15.5	1.1903
1.4	0.1461	0.371	0.238	30	1.4771
1.85	0.2672	0.848	0.484	26	1.4150
1.5	0.1761	0.443	0.286	20	1.3010
1.6	0.2041	0.519	0.357	33	1.5185
1.95	0.2900	0.888	0.517	41	1.6128
1.3	0.1139	0.264	0.191	23.5	1.3711
1.45	0.1614	0.420	0.265	27.5	1.4393
5.2	0.7160	12.65	4.85	495	2.6946
4.95	0.6946	10.5	3.87	408	2.6107
4.9	0.6902	10.85	4.07	415	2.6180

7°/oo, 25°C cont.

length	log length	wet wt.	dry wt.	org.c	log c.
5.0	0.6990	11.1	4.28	460	2.6628
5.25	0.7202	10.65	5.17	568	2.7543
5.0	0.6990	9.3	4.0	375	2.5740
5.5	0.7404	12.0	5.47	575	2.7597
5.3	0.7243	10.7	4.78	415	2.6180
4.85	0.6857	9.0	3.66	490	2.6902
4.85	0.6857	9.85	4.50	515	2.7118
2.2	0.3424	1.5	0.728	76.5	1.8837
1.95	0.2990	1.05	0.541	67.5	1.8293

7°/oo, 30°C.

1.5	0.1761			12.0	1.0792
1.55	0.1903			13.5	1.1303
1.65	0.2175			15.0	1.1761
1.45	0.1614	0.358	0.232	20.0	1.3010
1.35	0.1303	0.255	0.193	19.5	1.2900
1.15	0.0607	0.148	0.120	10.0	1.0000
5.0	0.6990	10.25	3.?	400	2.6021
4.35	0.6385	7.12	2.62	280	2.4472
4.95	0.6946	9.79	3.18	300	2.4771
4.15	0.6180	6.4	2.88	382	2.5821
3.15	0.4983	3.67	1.86	200	2.3010
3.7	0.5682	4.88	2.08	205	2.3118
3.75	0.5740	5.72	2.50	220	2.3424
4.0	0.6021	4.93	3.47	172	2.2355
3.95	0.5966	6.19	2.50	255	2.4065
4.0	0.6021	5.87	2.36	230	2.3617
2.35	0.3711	1.5	0.673	85	1.9294
1.75	0.2430	0.705	0.364	53.5	1.7284

14°/oo, 5°C.

length	log length	wet wt.	dry wt.	org. c.	log c.
1.1	0.0414	0.13	0.126	7.5	0.8751
1.55	0.1761	0.407	0.295	24	1.3802
2.1	0.3222	0.997	0.660	82.5	1.9165
1.7	0.2304	0.521	0.355	46.5	1.6675
1.65	0.2175	0.583	0.420	52.5	1.7202
1.55	0.1903	0.533	0.316	39	1.5911
1.4	0.1361	0.346	0.238	27	1.4314
1.55	0.1903	0.535	0.337	41	1.6128
2.1	0.3222		0.580	80	1.9031
2.85	0.4548		1.10	139	2.1430
2.25	0.3522		0.697	84	1.9243
2.4	0.3802		0.758	94	1.9731
1.95	0.2900		0.538	68	1.8325
1.85	0.2672		0.430	58	1.7634
2.25	0.3522		0.617	78	1.8921

14°/oo, 10°C.

1.05	0.1202			6.5	0.8129
1.25	0.0969			12	1.0792
1.6	0.2175			37	1.5682
1.4	0.1461			28.5	1.4548
1.25	0.0969			20	1.3010
1.1	0.0414	0.262	0.135	11.5	1.0607
1.0	0.0000	0.177	0.106	8.5	0.9294
1.05	0.0212	0.219	0.123	9.5	0.9777
1.0	0.0000	0.141	0.100	8.5	0.9294
1.5	0.1761	0.531	0.311	29	1.4624
2.8	0.4472	2.24	1.09	130	2.1139
3.3	0.5185	3.28	1.49	197	2.2945
2.8	0.4472	2.41	1.10	130	2.1139
4.15	0.6180	5.78	2.61	305	2.4843
4.25	0.6284	5.8	2.51	280	2.4472
3.75	0.5740	4.00	1.83	197	2.2945
3.5	0.5441	3.71	1.73	180	2.2553

14°/oo, 10°C cont.

length	log length	wet wt.	dry wt.	org.c.	log c.
3.9	0.5911	5.31	2.33	250	2.3979
4.15	0.6180	6.87	2.72	367	2.4871
4.25	0.6284	7.42	2.68	305	2.4843
4.45	0.6484	8.41	3.02	390	2.5911
4.55	0.6580	8.42	3.09	362	2.5587
1.85	0.2672		0.504	55	1.7404
2.1	0.3222		0.117	52	1.7160
1.85	0.2672		0.473	52	1.7160
1.8	0.2553		0.436	34	1.5315
1.9	0.2788		0.590	49	1.6902
2.3	0.3617		0.930	79.5	1.9004
2.35	0.3711		0.952	79.5	1.9004
2.25	0.3522		0.853	73.5	1.8663

14°/oo, 15°C.

1.2	0.0792	0.317	0.195	14	1.1461
1.45	0.1614	0.528	0.310	20.5	1.3118
1.35	0.1303	0.375	0.249	19	1.2788
1.25	0.0969	0.283	0.190	14.5	1.1614
1.0	0.0000	0.153	0.108	11	1.0414
2.35	0.3711	1.44	0.823	78	1.8921
2.3	0.3617	1.7	0.848	72	1.8573
1.8	0.2553	0.87	0.523	36.5	1.5623
1.85	0.2672	0.876	0.526	29	1.4624
2.8	0.4472	2.41	1.10	130	2.1139
3.3	0.5185	3.71	1.69	187	2.2718
2.5	0.3979	1.82	0.86	115	2.0607
4.5	0.6532	8.02	3.05	325	2.5105
4.25	0.6284	6.86	2.60	240	2.3802
4.55	0.6580	8.52	3.10	356	2.5514
4.4	0.6484	7.65	2.96	255	2.4065
4.85	0.6857	9.43	3.46	347	2.5403
5.0	0.6990	11.3	4.3	425	2.6284
5.0	0.6990	10.2	3.43	342	2.5340
4.75	0.6767	9.61	3.33	395	2.5966

14°/oo, 25°C.

length	log length	wet wt.	dry wt.	org.c.	log c.
1.45	0.1614	0.487	0.289	17	1.2304
1.15	0.0607	0.227	0.154	9	0.9542
1.4	0.1461	0.351	0.226	15	1.1761
1.45	0.1614	0.479	0.292	20	1.3010
1.45	0.1614			32	1.5051
1.1	0.0414			12.5	1.0969
1.0	0.0000	0.123	0.118	12	1.0792
5.05	0.7033	10.800	4.06	428	2.6314
5.3	0.7243	12.0	4.51	435	2.6385
5.1	0.7076	10.5	4.98	508	2.7059
4.85	0.6857	9.5	3.93	487	2.6875
5.30	0.7234	10.60	4.68	435	2.6385
5.0	0.6990	8.65	3.48	395	2.5966
5.25	0.7202	10.35	4.76	427	2.6304
4.65	0.6675	7.85	3.28	308	2.4886
4.65	0.6675	7.0	3.11	360	2.5563
5.10	0.7076	8.85	4.27	482	2.6830
2.4	0.3802	1.85	0.806	83.5	1.9217
2.0	0.3010	1.07	0.541	62	1.7924
2.0	0.3010	1.2	0.567	67.5	1.8293

14°/oo, 30°C.

1.45	0.1614			13	1.1139
1.65	0.2175			22	1.3424
1.0	0.0000	0.104	0.100	11	1.0414
1.75	0.2430	0.600	0.398	38	1.5798
1.35	0.1303	0.301	0.240	18.5	1.2672
4.7	0.6721	8.75	3.12	310	2.4914
4.3	0.6335	7.04	2.60	335	2.5250
5.25	0.7202	11.65	4.0	415	2.6180
4.5	0.6530	8.26	2.86	295	2.4698
4.1	0.6128	5.65	2.25	250	2.3979
3.6	0.5563	4.2	1.78	150	2.1761
3.35	0.5250	3.83	1.67	180	2.2553

14°/oo, 30°C cont.

length	log length	wet wt.	dry wt.	org.c.	log c.
3.65	0.5623	4.54	1.91	180	2.2553
4.0	0.6021	5.75	2.22	190	2.2788
3.8	0.5798	4.8	2.05	232	2.3655
1.8	0.2553	0.875	0.483	60.5	1.7818
1.75	0.2430	0.689	0.382	52.5	1.7202

21°/oo, 5°C.

1.3	0.1139	0.293	0.231	19	1.2788
1.4	0.1461	0.404	0.275	32.5	1.5119
1.2	0.0792	0.291	0.205	29	1.4624
1.1	0.0414	0.321	0.168	22	1.3424
1.15	0.0607	0.271	0.211	23	1.3617
1.15	0.0607	0.227	0.171	19	1.2788
1.85	0.2672		0.482	58	1.7634
1.45	0.1614		0.267	38	1.5798
2.1	0.3222		0.671	65.5	1.8162
1.65	0.2175		0.386	45.5	1.6580
1.95	0.2900		0.500	65.5	1.8160
1.75	0.2430		0.416	52	1.7160

21°/oo, 10°C.

1.3	0.1139			15	1.1761
1.5	0.1761			23.5	1.3711
1.1	0.0414			10	1.0000
1.4	0.1464	0.464	0.255	20	1.3010
1.35	0.1303	0.370	0.209	19	1.2788
1.35	0.1303	0.431	0.217	24	1.3802
1.05	0.0212	0.208	0.116	13.5	1.1303
1.0	0.0000	0.178	0.100	9.5	0.9777
1.85	0.2672		0.434	43	1.6335
1.8	0.2553		0.410	37.5	1.5740
1.5	0.1761		0.30	32	1.5051

21°/oo, 10°C cont.

length	log length	wet wt.	dry wt.	org.c.	log c.
2.65	0.4232	1.95	0.963	130	2.1139
2.6	0.4150	1.81	0.921	122	2.0864
4.2	0.6232	5.66	2.31	270	2.4314
3.25	0.5119	2.58	1.21	136	2.1303
3.15	0.4983	2.51	1.21	155	2.1903
4.0	0.6021	4.7	2.1	215	2.3324
4.0	0.6021	3.98	2.21	252	2.4014
3.65	0.5623	5.81	2.09	260	2.4150
4.25	0.6284	7.88	2.77	278	2.4440
4.6	0.6628	8.81	3.21	380	2.5798

21°/oo, 15°C.

1.55	0.1903	0.568	0.330	22	1.3424
1.65	0.2175	0.582	0.337	28	1.4472
1.4	0.1461	0.404	0.240	20	1.3010
2.45	0.3892	1.69	0.95[illegible]	79.5	1.9004
3.7	0.5682	4.55	1.72	194	2.2878
4.2	0.623[illegible]	7.04	2.65	240	2.3802
4.0	0.6021	5.81	2.42	225	2.3522
3.75	0.5740	4.84	1.82	145	2.1614
2.8	0.4472	2.72	1.2	137	2.1367
4.15	0.6180	6.14	2.48	243	2.3856
4.7	0.6721	9.12	3.54	448	2.6513
4.55	0.6580	8.50	2.86	310	2.4915
4.55	0.6580	9.40	3.48	367	2.5647
4.75	0.6767	8.77	2.92	290	2.4624

21°/oo, 25°C.

length	log length	wet wt.	dry wt.	org.c.	log c.
1.4	0.1461	0.420	0.258	17	1.2304
1.2	0.0792	0.268	0.177	16	1.2041
1.25	0.0969	0.281	0.189	13.5	1.1303
1.25	0.0969			15	1.1761
1.35	0.1303			13.5	1.1303
1.3	0.1139			10.5	1.0212
1.3	0.1139			12.5	1.0969
1.15	0.0607	0.186	0.150	9	0.9542
1.4	0.1614	0.383	0.256	19.5	1.2900
5.25	0.7202	11.15	4.38	448	2.6513
5.5	0.7404	13.6	5.43	515	2.7118
6.1	0.7853	15.4	6.58	640	2.8062
4.05	0.6075	5.0	2.42	195	2.2900
4.5	0.6532	7.28	3.17	360	2.5563
4.7	0.6721	7.25	3.31	328	2.5159
4.85	0.6857	8.03	3.30	310	2.4914
5.3	0.7243	10.75	4.92	450	2.6532
5.1	0.7076	10.95	4.92	515	2.7118
1.75	0.2430	0.83	0.468	72	1.8573

21°/oo, 30°C

1.1	0.0414	0.132	0.122	10	1.0000
1.35	0.1303	0.249	0.205	12.5	1.0969
1.5	0.1761	0.268	0.245	11.5	1.0607
1.35	0.1303	0.262	0.209	15	1.1903
4.45	0.6484	8.0	3.09	350	2.5441
3.1	0.4914	6.16	1.35	145	2.1614
2.8	0.4472	2.25	1.06	95	1.9777
3.15	0.4969	3.57	1.55	122	2.0864
2.7	0.4314	2.48	1.09	100	2.0000
3.75	0.5740	5.11	2.98	150	2.1761
4.05	0.6075	6.67	2.45	210	2.3222
3.25	0.5105	3.75	1.57	145	2.1614

21°/oo, 30°C cont.

length	log length	wet wt.	dry wt.	org.c.	log c.
3.36	0.5250	3.70	1.52	155	2.1903
3.15	0.4983	3.53	1.45	130	2.1139
1.6	0.2041	0.686	0.372	48	1.6812
1.95	0.2900	1.05	0.540	69	1.8388
1.55	0.1903	0.443	0.258	17	1.2304
1.5	0.1761	0.504	0.399	26.5	1.4232
2.25	0.3502	1.23	0.651	65.5	1.8162
2.0	0.3010	0.97	0.560	69.5	1.8420

28°/oo, 5°C.

1.7	0.2304	0.734	0.472	59.5	1.7745
1.1	0.0414	0.262	0.176	20.5	1.3118
1.45	0.1614	0.449	0.296	39.5	1.5966
1.45	0.1614	0.445	0.296	41	1.6128
1.3	0.1139	0.327	0.231	17.5	1.2430
1.05	0.0212	0.195	0.149	21.5	1.3324
1.3	0.1139		0.231	30.5	1.4843
1.75	0.2430		0.496	58	1.7634

28°/oo, 10°C.

1.45	0.1614	0.503	0.266	36	1.5563
1.75	0.2430	0.837	0.409	56	1.7482
1.45	0.1614	0.502	0.267	40.5	1.6075
1.4	0.1461	0.497	0.278	39.5	1.5966
1.75	0.2430	1.02	0.493	59	1.7709
1.75	0.2430	0.85	0.420	53.5	1.7280
1.9	0.2900	0.99	0.452	56	1.7520
2.7	0.4314	1.98	1.09	150	2.1761
2.75	0.4393	2.33	1.20	145	2.1614
2.7	0.4314	2.29	1.15	130	2.1139
2.75	0.4393	2.4	1.23	145	2.1614
2.85	0.4548	2.37	1.27	160	2.2041
1.9	0.2788	1.06	0.53	57	1.7559
2.0	0.3010	1.03	0.517	75	1.8751
2.65	0.4232	2.48	1.08	112	2.0492

21°/oo, 30°C cont.

length	log length	wet wt.	dry wt.	org.c.	log c.
3.36	0.5250	3.70	1.52	155	2.1903
3.15	0.4983	3.53	1.45	130	2.1139
1.6	0.2041	0.686	0.372	48	1.6812
1.95	0.2900	1.05	0.540	69	1.8388
1.55	0.1903	0.443	0.258	17	1.2304
1.5	0.1761	0.504	0.399	26.5	1.4232
2.25	0.3502	1.23	0.651	65.5	1.8162
2.0	0.3010	0.97	0.560	69.5	1.8420

28°/oo, 5°C.

1.7	0.2304	0.734	0.472	59.5	1.7745
1.1	0.0414	0.262	0.176	20.5	1.3118
1.45	0.1614	0.449	0.296	39.5	1.5966
1.45	0.1614	0.445	0.296	41	1.6128
1.3	0.1139	0.327	0.231	17.5	1.2430
1.05	0.0212	0.195	0.149	21.5	1.3324
1.3	0.1139		0.231	30.5	1.4843
1.75	0.2430		0.496	58	1.7634

28°/oo, 10°C.

1.45	0.1614	0.503	0.266	36	1.5563
1.75	0.2430	0.837	0.409	56	1.7482
1.45	0.1614	0.502	0.267	40.5	1.6075
1.4	0.1461	0.497	0.278	39.5	1.5966
1.75	0.2430	1.02	0.493	59	1.7709
1.75	0.2430	0.85	0.420	53.5	1.7280
1.9	0.2900	0.99	0.452	56	1.7520
2.7	0.4314	1.98	1.09	150	2.1761
2.75	0.4393	2.33	1.20	145	2.1614
2.7	0.4314	2.29	1.15	130	2.1139
2.75	0.4393	2.4	1.23	145	2.1614
2.85	0.4548	2.37	1.27	160	2.2041
1.9	0.2788	1.06	0.53	57	1.7559
2.0	0.3010	1.03	0.517	75	1.8751
2.65	0.4232	2.48	1.08	112	2.0492

28°/oo, 15°C.

length	log length	wet wt.	dry wt.	org.c.	log c.
1.25	0.0969	0.325	0.216	21	1.3222
1.9	0.2788	0.841	0.520	30	1.4771
1.8	0.2553	0.750	0.488	30.5	1.4843
3.15	0.4983	3.39	1.45	153	2.1847
2.85	0.4548	2.22	0.97	95	1.9777
4.0	0.6021	5.95	2.33	223	2.3483
3.6	0.5563	4.85	1.93	194	2.2878
3.95	0.5966	5.78	2.26	225	2.3522
3.0	0.4771	2.99	1.30	161	2.2068
3.65	0.5623	4.79	1.98	216	2.3345
3.4	0.5315	4.21	1.55	152	2.1818
1.5	0.1761	0.535	0.294	39.5	1.5966
1.55	0.1903	0.630	0.352	45	1.6532
2.0	0.3010	1.09	0.531	65.5	1.8162
1.35	0.1303	0.397	0.228	34.5	1.5378

28°/oo, 25°C.

1.0	0.0000	0.142	0.105	10	1.0000
1.3	0.1139	0.321	0.208	15	1.1761
1.05	0.0212	0.283	0.187	25	1.3979
1.05	0.0212	0.216	0.141	22	1.3424
1.75	0.2430	1.05	0.502	56	1.7483
2.35	0.3711	1.34	0.755	47	1.6721

28°/oo, 30°C.

1.8	0.2553	0.892	0.514	62	1.7924
1.25	0.0969	0.336	0.206	55	1.7404
1.4	0.1461	0.484	0.367	45.5	1.6580
3.05	0.4843	3.52	1.49	137	2.1367
2.0	0.3010	1.22	0.59	60	1.7782

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