THE CONSTRUCTION OF ENERGY BUDGETS FOR THREE INTERTIDAL ROCKY SHORE GASTROPODS

Patella vulgata, *Littorina littoralis* and *Nucella lapillus*

by

John Richard Wright, B.Sc.

Department of Marine Biology,
(University of Liverpool),
Port Erin,
Isle of Man.

December, 1976.

To Linda

CONTENTS

page

ACKNOWLEDGEMENTS

SUMMARY

CHAPTER 1 GENERAL INTRODUCTION 1

CHAPTER 2 GROWTH PRODUCTION

Introduction 5

Patella vulgata 6

Littorina littoralis 29

Nucella lapillus 38

CHAPTER 3 REPRODUCTIVE PRODUCTION

Introduction 53

Patella vulgata 53

Littorina littoralis 67

Nucella lapillus 70

CHAPTER 4 RESPIRATION 76

CHAPTER 5 INGESTION AND EGESTION

Introduction 91

Patella vulgata 91

Littorina littoralis 100

Nucella lapillus 107

CHAPTER 6 ENERGY BUDGETS 119

REFERENCES 128

APPENDIX 1

APPENDIX 2

ACKNOWLEDGEMENTS

I should like to express my sincere gratitude to my supervisor, Dr. R.G. Hartnoll, for his advice and encouragement throughout this work. I also wish to thank Professor E. Naylor for providing laboratory facilities at the Department of Marine Biology, and Liverpool University for financial support.

I am grateful to the staff, research students and technicians at the Department of Marine Biology for assistance on many occasions.

SUMMARY

Energy budgets were constructed for populations of Patella vulgata, Littorina littoralis and Nucella lapillus, situated on a M.T.L. carboniferous limestone ledge at Derbyhaven, Isle of Man. The energy budget of a population may be summarized by the equation

$C = P + R + F + U$ where $P = Pr + Pg$

Each component was measured in kilocalories per annum. C, energy content of the food consumed; P, total energy produced as flesh (Pg) and gametes (Pr); R, energy lost due to metabolism; F, energy lost due to faeces; U, energy lost due to urine and other exudates.

To construct the energy budgets it was necessary to measure the following parameters: biomass, growth, mortality, recruitment, fecundity, respiration, food intake and excretion. These were measured by a combination of field and laboratory studies.

Biomass and growth: Patella vulgata is relatively sedentary, with feeding excursions occurring when immersed during the day. Therefore individuals are present at predictable locations at certain times of the day. Five one metre square quadrats in a continuous row parallel to the water's edge were marked out at mid-tide level. Nucella lapillus is an active animal and does not return to predictable locations. However this animal tends to remain in localized areas, congregating in cracks during cold and rough weather, and moving out onto the rock face during feeding excursions. An area of approximately 12 m^2 with naturally defined boundaries was studied. Littorina littoralis is an active animal and does not return to any predictable location. It feeds on the fucoid algae upon which it is fairly uniformly distributed in the sampling area. Each month ten 100 g. dry weight samples of Fucus serratus and Fucus vesiculosus were collected from the same ten locations. Monthly measurements of shell length at each sampling site were converted to biomass and dry weight, using conversion

graphs derived from samples taken nearby. In addition calorific values were determined using a Phillipson micro-bomb calorimeter. Growth estimates were estimated by measuring marked animals which were recaptured at monthly intervals.

Fecundity: For each species monthly determinations were made of gonadal weight and condition. Also egg masses of Littorina littoralis attached to the fucoids were removed and weighed.

Respiration: The aerial and aquatic respiration of the three species were measured frequently, using Gilson and Davies volumetric respirometers to measure aerial respiration and the micro-Winkler technique for aquatic respiration.

Feeding and excretion: Open caged slates were bolted onto the rock surface and when sufficient algal film was present limpets were placed on the slates and the area grazed recorded to give estimates of food intake. Similar plates were used in the laboratory to obtain weight estimates for faecal production and estimates of urine output by the Berthelot procedure. Laboratory estimates were also made for food uptake by Nucella feeding on barnacles and Littorina littoralis feeding on Fucus.

All the parameters of the energy budget equation were measured and the following equations derived.

$$C = P + R + F + U \qquad \text{where } P = Pr + Pg$$

C is the summation of $P + R + F + U$ and C_1 is the measured value.

P. vulgata Kcals/m^2/yr

1974 $563.29\ (C) = 36.58 + 115.66 + 410.64 + 0.42$

where $P = 22.72 + 13.86$

$570.6\ (C_1)$

1975 $606.02\ (C) = 41.78 + 122 + 441.79 + 0.45$

where $P = 22.40 + 18.88$

$602.0\ (C_1)$

L. littoralis   Kcals/kg. dry wt. fuccid/yr

1975   235.95 (C) = 55.27 + 116.53 + 63.86 + 0.29

where P = 19.89 + 35.38

234.04 (C_1)

N. lapillus   Kcals/m^2/yr

1975   29.34 (C) = 5.94 + 18.17 + 5.23 (F + U) where P = 0.68 + 5.26

32.11 (C_1)

CHAPTER 1

– INTRODUCTION

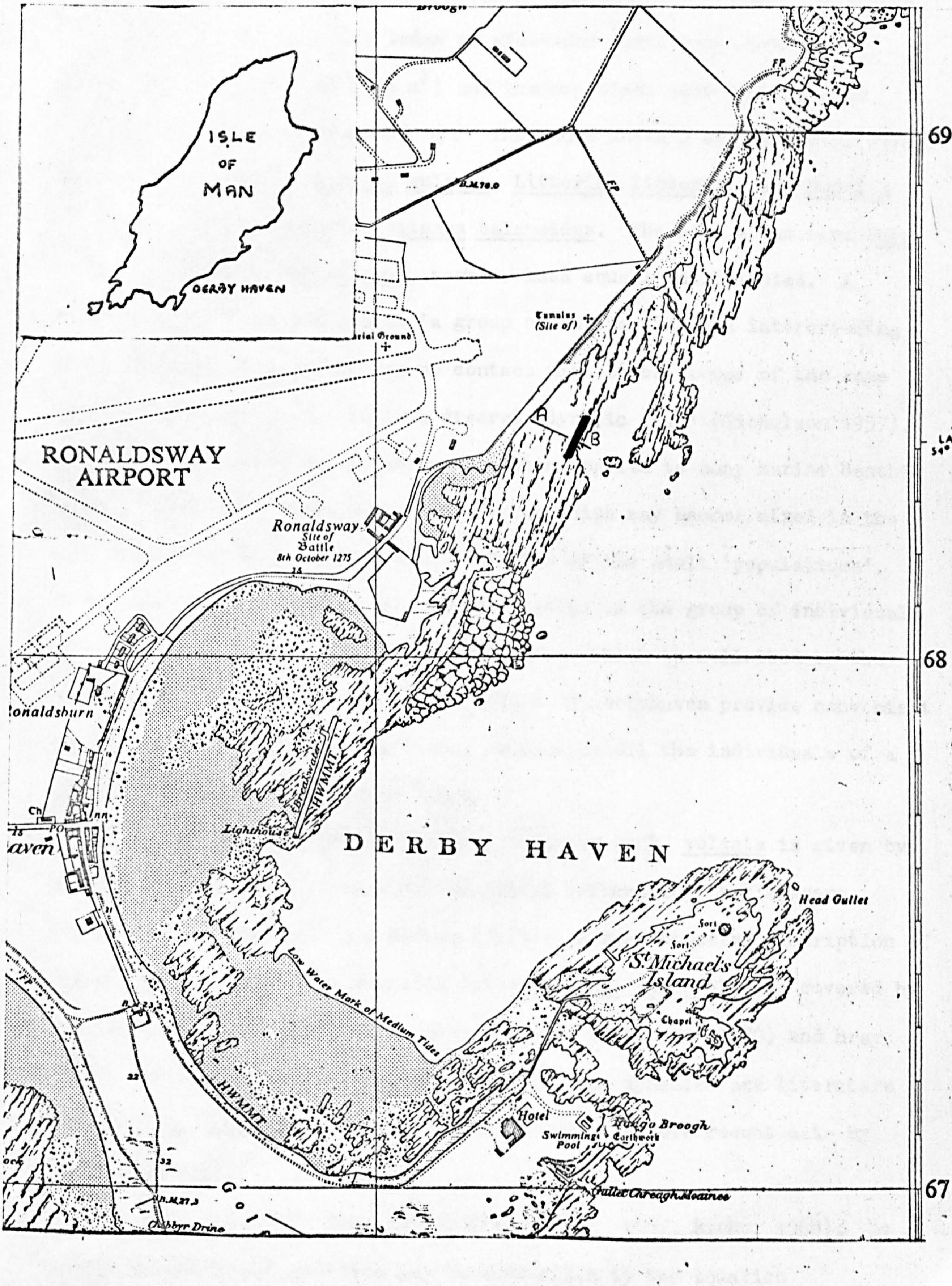
Ecological energetics can be a useful approach with which to assess the importance of a species' contribution to the structure, productivity and functioning of a community (Macfadyen 1963, Odum 1963, Slobodkin 1962). Calculations based on energy patterns have been used to suggest factors controlling seasonal patterns of occurrence (Anraku 1964), the degree to which subpopulations are energy limited (Paine 1965) and the extent to which a generalized resource is drawn on by set consumers (Odum et al. 1962). Theoretical consideration of ecological energetics has been treated fully by Lindemann (1942), Phillipson (1966), Odum (1963) and Slobodkin (1962); however the paucity of field data emphasizes the need for more research (Engelmann 1966).

There is a lack of literature on the energy budgets of marine organisms especially intertidal animals, though recently studies have been completed on soft substrate animals. Only one previous study on a rocky-shore animal, Scrobicularia plana (Hughes 1970), has independently estimated each component of the energy budget from laboratory and field data. This lack of work on energy budgets is very surprising as extensive literature is available on the general ecology and population dynamics of many rocky-shore animals. To advance further the understanding of the ecology and population dynamics of these animals further information on energy budgets is necessary.

Therefore it was decided to study three rocky-shore animals of ecological significance, the common limpet, Patella vulgata, and the flat periwinkle, Littorina littoralis, since the balance of the grazer/algae relationship determines the local and temporal character of much of the rocky littoral, and the common dog-whelk, Nucella lapillus, a major littoral carnivore.

The rocky shore chosen for this energetics study was Derbyhaven, Isle of Man (co-ordinates 295 695, Fig.1), because the shore is fairly

Fig.1. A section of the ordnance survey sheet sc 26 NE, Scale 6 Inches to 1 Mile, showing the position of study area(▬) and profile (AB).


ISLE OF MAN
DERBY HAVEN
RONALDSWAY AIRPORT
Broogh
B.M.78.0
F.P.
Tumulus (Site of)
Burial Ground
A
B
Ronaldsway Site of Battle 8th October 1275
Ronaldsburn
Ch
P.O.
Haven
Lighthouse
Breakwater
HWMMT
DERBY HAVEN
Low Water Mark of Medium Tides
HWMMT
Head Gullet
Fort
Fort
St Michael's Island
Chapel
Hotel
Swimming Pool
Hango Broogh Earthwork
Gullet Chreagh Moainee
B.M.27.3
Chibbyr Drine
69
68
67
LAT 54° 05'

sheltered, point 5 on Ballantine's exposure scale, and relatively isolated from man's interference. The limestone strata are almost horizontal, and in the intertidal area present a series of platforms or ledges descending in steps (Fig. 2 & 3). The ledge at mid-tidal level was approximately 110 m long by 6.5 m wide (715 m^2) and the organisms were more or less uniformly distributed (Fig. 4 & 5). The major animals at this level were the three gastropods, *Patella vulgata*, *Littorina littoralis* and *Nucella lapillus*, and the barnacle, *Balanus balanoides*. The main algae were *Fucus serratus* and *Fucus vesiculosus*, more or less equally distributed. A population has been defined as 'a group of interacting and interbreeding individuals which normally has no contact with other groups of the same species. That is to say it is a discrete dynamic unit' (Nicholson 1957). However, this definition is too narrow when applied to many marine benthic invertebrates which have planktonic larvae which may become mixed in the sea, thus preventing reproductive isolation of the adult 'populations'. It is convenient to assign the term population to the group of individuals of a species living within an area of sea bed which is delimited by the study in hand (Hughes 1970). These ledges at Derbyhaven provide convenient delimited areas and a population was defined as all the individuals of a species living on a particular ledge.

A comprehensive review of the literature on *P. vulgata* is given by Ballantine (1961) and subsequent additional information by Blackmore (1969a, 1969b) and Lewis and Bowman (1975). A comprehensive description of the general ecology and population dynamics of *L. littoralis* is covered by the studies of Barkmann(1955), Bakker (1959), Guiterman (1970) and Bray (1974). A comprehensive study of the population dynamics and literature review of *N. lapillus* is given by Feare (1969) and more recent data by Crothers (1974).

Following I.B.P. terminology (Petrusewic 1967, Ricker 1968), the energy budget of a population may be summarized by the equation

Fig. 2. Profile of the rocky shore at Derbyhaven along the line AB in Fig. 1. The approximate ranges (—) of the important species are marked.

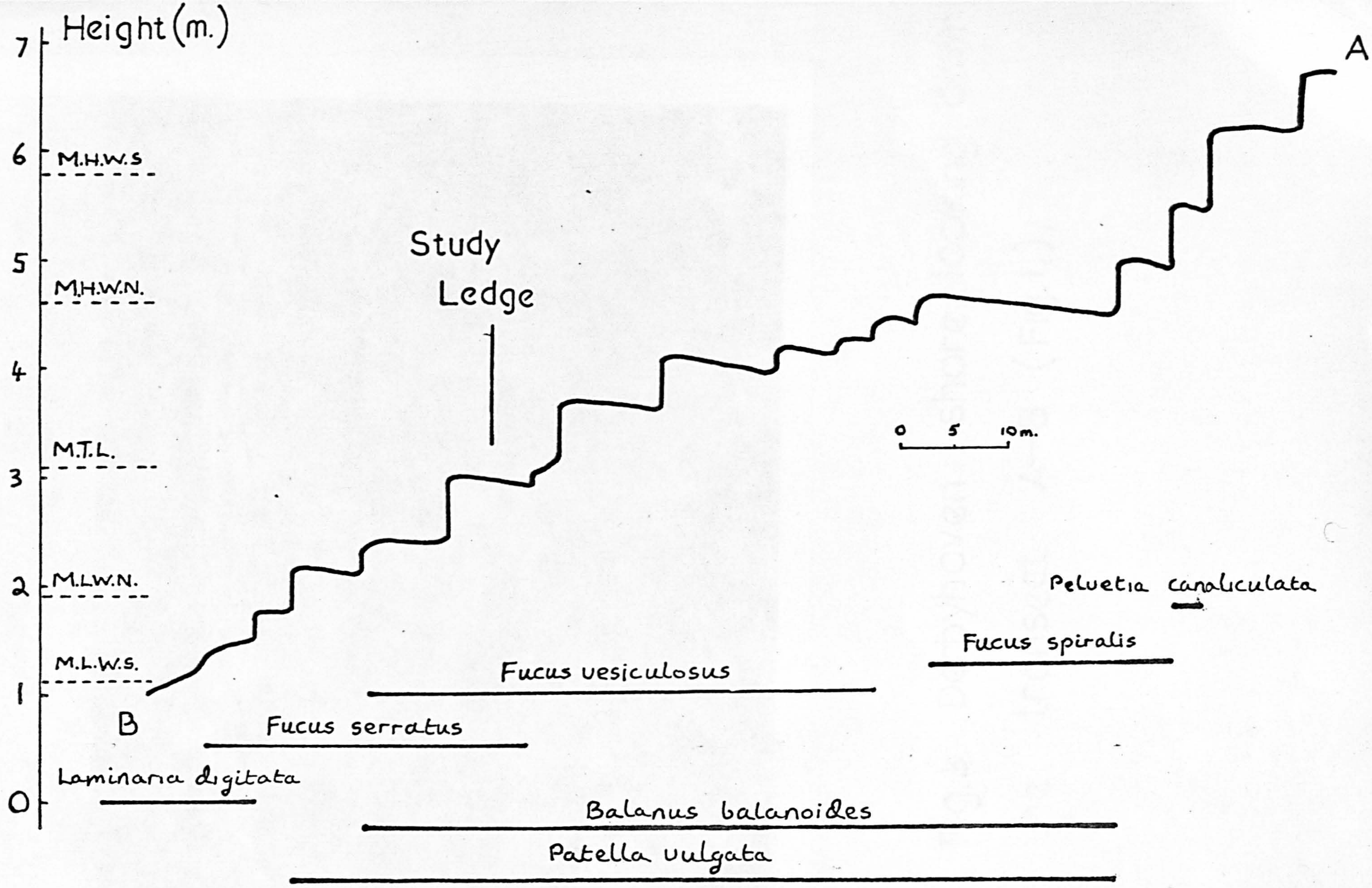

Height (m.)
7
6
5
4
3
2
1
0
M.H.W.S
M.H.W.N.
M.T.L.
M.L.W.N.
M.L.W.S.
A
B
Study Ledge
0 5 10m.
Pelvetia canaliculata
Fucus spiralis
Fucus vesiculosus
Fucus serratus
Laminaria digitata
Balanus balanoides
Patella vulgata

Fig.3. Derbyhaven shore, looking down the transect A—B (Fig.1.).

Fig. 4. study ledge.

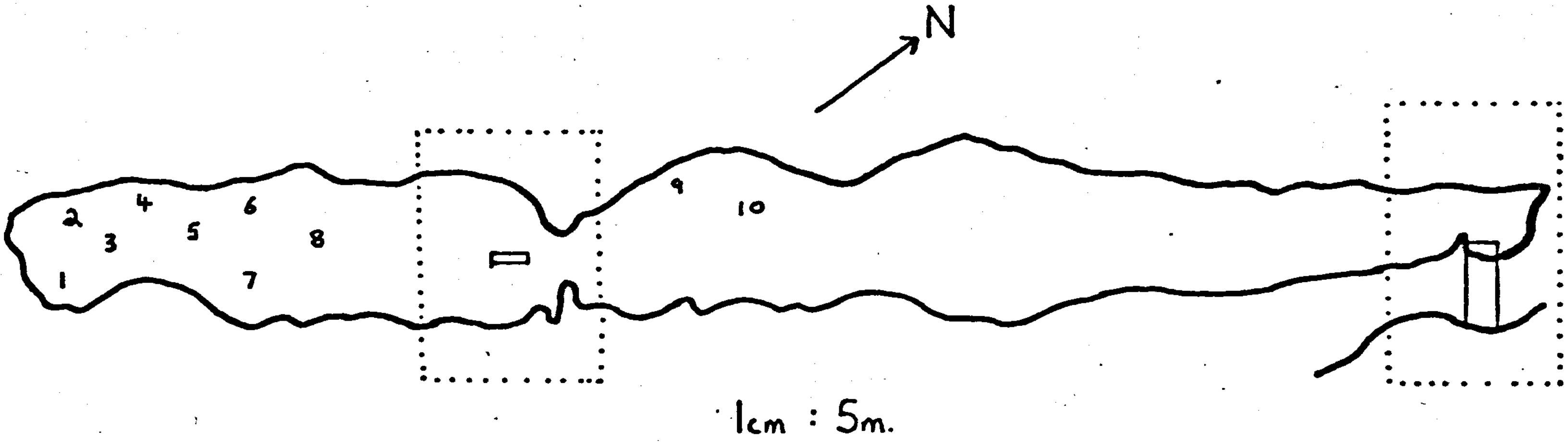


Fig. 5. Sketch of the study ledge at M.T.L. The numbers indicate where the ten fucoid samples were obtained, ▭ is the position of the quadrats, ▯ the dogwhelk area & ⬚ the area where no biological material was removed.

$$C = P + R + F + U$$

where $P = Pr + Pg$.

Each component may be measured in kilocalories per annum . C, energy content of the food consumed by the population; P, total energy produced by the population as flesh or gametes; Pg, energy content of the tissue added to the population due to growth and recruitment; Pr, energy content of the gametes liberated during spawning; R, energy lost to the population due to metabolism (represented by respiration); F, energy leaving the population as faeces; U, energy lost via excreted urine or other exudates. C - F is that part of the food that is absorbed into the body through the wall of the alimentary canal. C - F - U is the proportion of ingested energy which is assimilated (A) by the population and has been called energy flow (Smalley 1960) or gross production (Engelmann 1966). P is termed net production by Engelmann (1966) but will be called production, following I.B.P. terminology. Energy loss via nitrogenous excretion and other exudates such as mucus secretion (U) has been assumed to be negligible in many studies and therefore has not been assessed, but nitrogenous excretion was measured in this study.

In many cases it has been impossible to estimate every component, especially ingestion, in the energy equation for a single species population, thus depriving the studies of internal checks on their accuracy (Odum & Smalley, 1959, Smalley 1960, Kuenzler 1961, Teal 1962, Golley & Gentry 1964, Mann 1965, Hughes 1971a, 1971b, Paine 1971, Trevallion 1971, Tenore et al. 1973, Dame 1976). In order to obtain maximum information on rates and efficiencies in the energy equation it is desirable to study populations in a steady-state condition. 'We restrict attention to steady states since seasonal differences in climate and physiology combined with essentially random meteorological or biological events in short term data collections will permit so much variance as to obscure real constancies and differences' (Slobodkin 1962). In the only previous rocky shore study of Scrobicularia plana (Hughes 1970), where all the components were estimated independently, the population unfortunately was not in steady-state condition. However the three populations in this study were in a steady state.

Knowledge of calorific contents in biological materials is an indispensable element of bioenergetic studies on account of the necessity to express all parameters of energy processes in comparable units, i.e. calories. In ecological literature, at least two concepts have been generally accepted to describe calorific value of biological materials, namely calories per gram of dry weight (cal/g dry), and calories per gram ash-free dry weight or calories per gram of organic weight (cal/g ash-free dry wt). Which of the two values cited by authors should be chosen for comparison? Richman (1958) discussing Ketchum and Redfield's (1949) data for chlorophycene suggests that calorific value of dry organic matter (ash-free volume) is less suitable for such comparisons since it has a higher variation due to varying ash content at the examined organisms. Golley (1961), being of a contrary opinion, says that calorific value per gram ash-free dry weight reflects more precisely the difference between materials that are to be compared than does calories per gram dry weight, on account of various admixtures. Dealing with plant material such as roots or litter, it is difficult to wash out the soil particles which bring about underestimation of calorific content per gram dryweight. Prus (1970) stated that when calculating general energy budgets the calorific value expressed in calories per gram by weight is quite sufficient. In this study calories per gram by weight were used, though calories per gram ash-free dry weight were given as well in some cases.

CHAPTER 2

GROWTH PRODUCTION

1. General Introduction

This chapter discusses the estimation of the growth production (Pg) in the energy equation over the course of the year for defined populations. The *P. vulgata* population was that within the quadrats (five 1 m^2), the *L. littoralis* as that per weight of fucoid (1 kg dry weight), and *N. lapillus* as that enclosed in the naturally defined area (approximately 12 m^2). The population limits are discussed more fully in the method sections of this chapter. There will be variation in population sizes during the year, but overall production will be balanced by mortality as the populations are in a steady-state condition.

The growth production is the energy content of the tissues added to the population due to growth and recruitment,

$$Pg = \Delta B + E$$

ΔB is the net increase in energy content of the standing crop, and E is the energy content of the individuals lost to the population through mortality. Therefore the following parameters were measured each month, somatic and shell weight (biomass minus gonads), growth rates, recruitment and mortality. The biomass refers to the energy content of the whole animal, the body tissue (the animal minus shell in gastropods) to the flesh, and the somatic tissue to the body minus gonads. The parameters were determined in dry weight (all weights unless otherwise stated in this study are dry weight) and converted to calories. When plotted on logarithmic scales the relationship between shell length and dry somatic weight and shell weight is linear, and so the regression of log weight on log length may readily be calculated. Regression equations for dry somatic tissue weight and shell weight against length were determined for the three species each month using measurements obtained from animals collected each month from the study ledge but away from the defined populations so as not to interfere. Thus by measuring each month the length of the population animals, and substituting them in the regressions, the somatic tissue and shell weights were calculated.

The monthly growth rates of the three populations were determined by the monthly increase in length of marked animals in the field and laboratory.

The recruitment and mortality were determined each month by the appearance and disappearance of animals which were recorded when the lengths of the animals in the defined populations were measured.

2. Patella vulgata

Introduction

The observations of various workers (Russell 1909, Orton 1928, Hatton 1936, 1938, Fischer-Piette 1941, 1946, 1948, Das & Seshappa 1948, Ballantine 1961, Choquet 1968, Blackmore 1969, Lewis & Bowman 1975) show that the growth and longevity of Patella vulgata depends on the habitat. The only constant observation is that the growth rate decreases with age, although some growth does continue throughout life.

The growth of the Derbyhaven limpets during the study period therefore had to be observed. There is no way of distinguishing year groups among larger limpets, nor do they in Britain have recognisable annual growth rings in their shells. Growth was therefore measured by following individual limpets over a period of time and noting the increase in size. All previous workers have used shell length as a measure of size in their studies of growth in P. vulgata. Shell length can be measured quickly and accurately, without disturbing the limpet. In theory, since relative shell height is known to vary, weight would be a better measurement of growth. However this is unpractical, as when limpets are lifted from their home the foot secretes large quantities of mucus and this appears to hinder reattachment; Ballantine (1961) observed that 5 - 10% failed to reattach successfully.

Previous workers have used various direct marking techniques to identify individual limpets so that their growth may be followed. It is possible that by marking the animals their behaviour or that of other animals may alter, e.g. the identifying mark may attract undue attention to it and possibly increase mortality. P. vulgata is relatively sedentary with feeding excursions only occurring when immersed by the tide during daylight hours (Hartnoll & Wright, in press) and thus individuals are present at predictable locations at the other times of the day. Therefore as the locations (homes) of the limpets are predictable the animals need not be marked.

Material and methods

The P. vulgata population studied was those animals within the quadrats. Five one metre square quadrats in a continuous row parallel to the water's edge were marked on the study ledge (Fig. 2,3 & 5). The length and position (home) of each limpet within the quadrats were recorded. This enabled each limpet to be located on subsequent inspections. At the beginning of each month the length of every quadrat limpet was measured to within 0.01 mm using vernier calipers.

Each month thirty limpets were collected from the study ledge but away from the quadrats. In the laboratory the limpet flesh was removed whole from its shell by dropping into boiling water for a few seconds. The gonads were dissected out and the somatic tissue dry weighed. Dry weight is the constant weight of the totally dehydrated body. The biological material in this study was dried to a constant weight by placing in an oven at 80°C for 48 hours. The ash content of biological material was obtained by incinerating dry weight samples in a muffle furnace at 500°C for four hours. The length and weight of the shells were measured. From the shell lengths, shell weights and somatic tissue weights of these animals, regression equations of log weight on log length were calculated, for shell and somatic tissue weights. The lengths of the quadrat limpets were substituted in the regression equations and their shell and somatic tissue weights obtained. The somatic tissue dry weights were converted to calories using the calorific values determined each month, from dry weight samples of the somatic tissue, using the Phillipson micro-bomb calorimeter (see appendix). The shell weight was converted to calories using a conversion factor. Vinogradov (1953) has given the percentage organic matter in the shell of another herbivorous marine gastropod, Turbo sp. as 1.1%. Paine (1971) used this percentage for the herbivorous gastropod Tegula funebralis and assumed that shell protein has a value of 5.7 Kcals/g. Using these figures the calorific content of these herbivorous gastropods is 0.0627 Kcals/g.

The limpets were individually recognisable so those missing or appearing each month were noted. It was assumed that immigration equalled emigration, therefore the monthly mortality was the difference between the loss and gain.

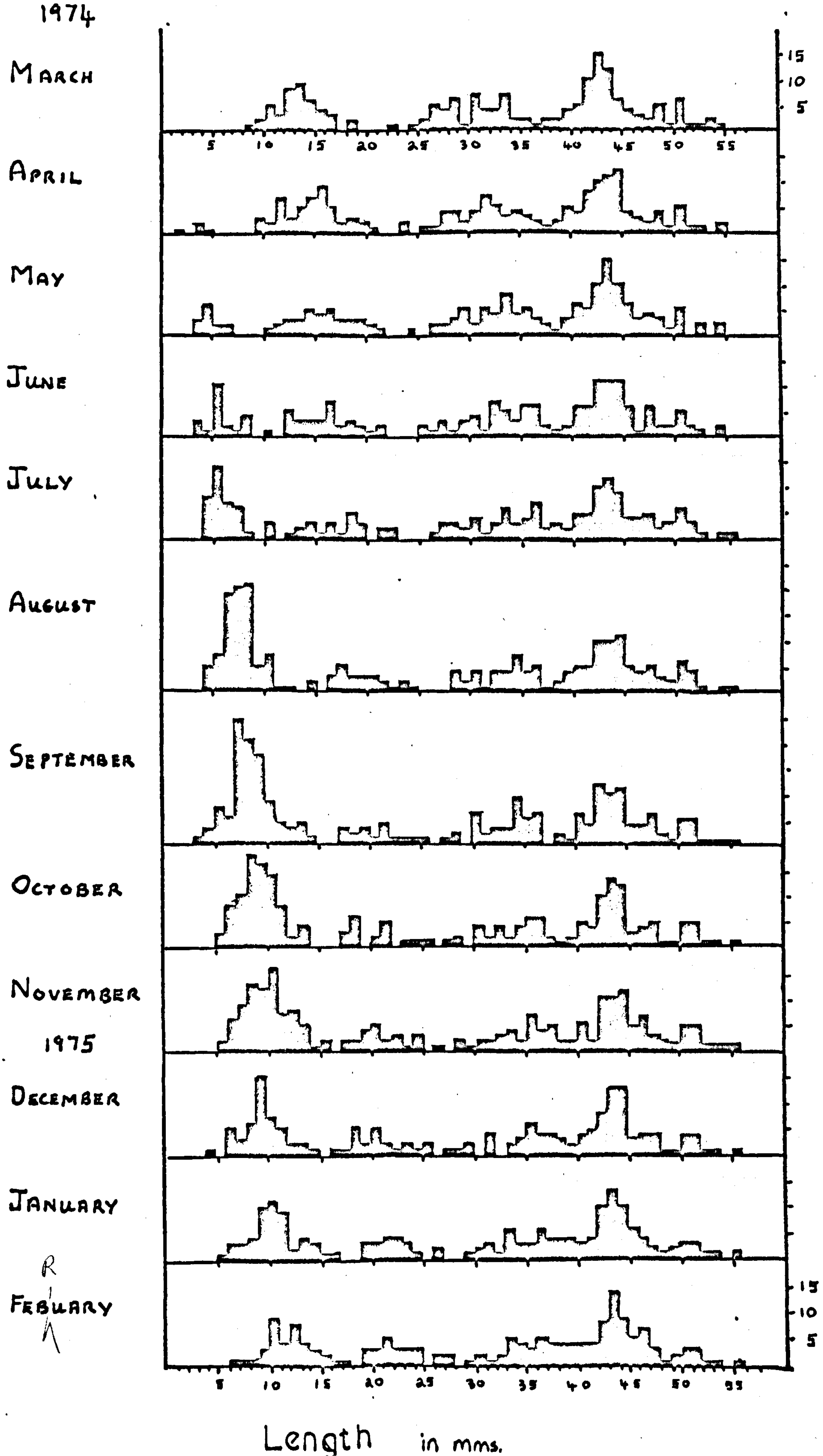
Results

a. Population analysis: Graphical representation of the data (Fig. 6 & 7) showed that for any month's collection the population was polymodal. Two or three distinct year groups can be observed (Fig. 8). The average monthly length of the P. vulgata 1974 and 1975 spat, second, third, fourth and fifth year animals of 1974 and also the maximum and minimum lengths of the spat, second and third years, are shown in Table 1.

The first spat were observed in early May in 1974 and early June in 1975. The minimum spat size observed in the quadrats was 2.44 mm. The spat numbers rapidly increased until in September 1974 there were 97 of which only 36 were present by March 1975. A similar pattern was observed in 1975, though the number of spat observed was much lower, a maximum of 31 in September falling to 15 by March 1976.

The second year animals also formed a complete and separate component within the total population. In March 1974 the average size was 13.00 mm ranging from 8 to 18 mm, and in 1975 was 12.4 mm ranging from 5 to 17 mm,

Fig. 6. The monthly length—frequency distribution of the P. vulgata quadrat population.


1974
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
1975
DECEMBER
JANUARY
R
FEBUARY
15
10
5
5
10
15
20
25
30
35
40
45
50
55
Length in mms.

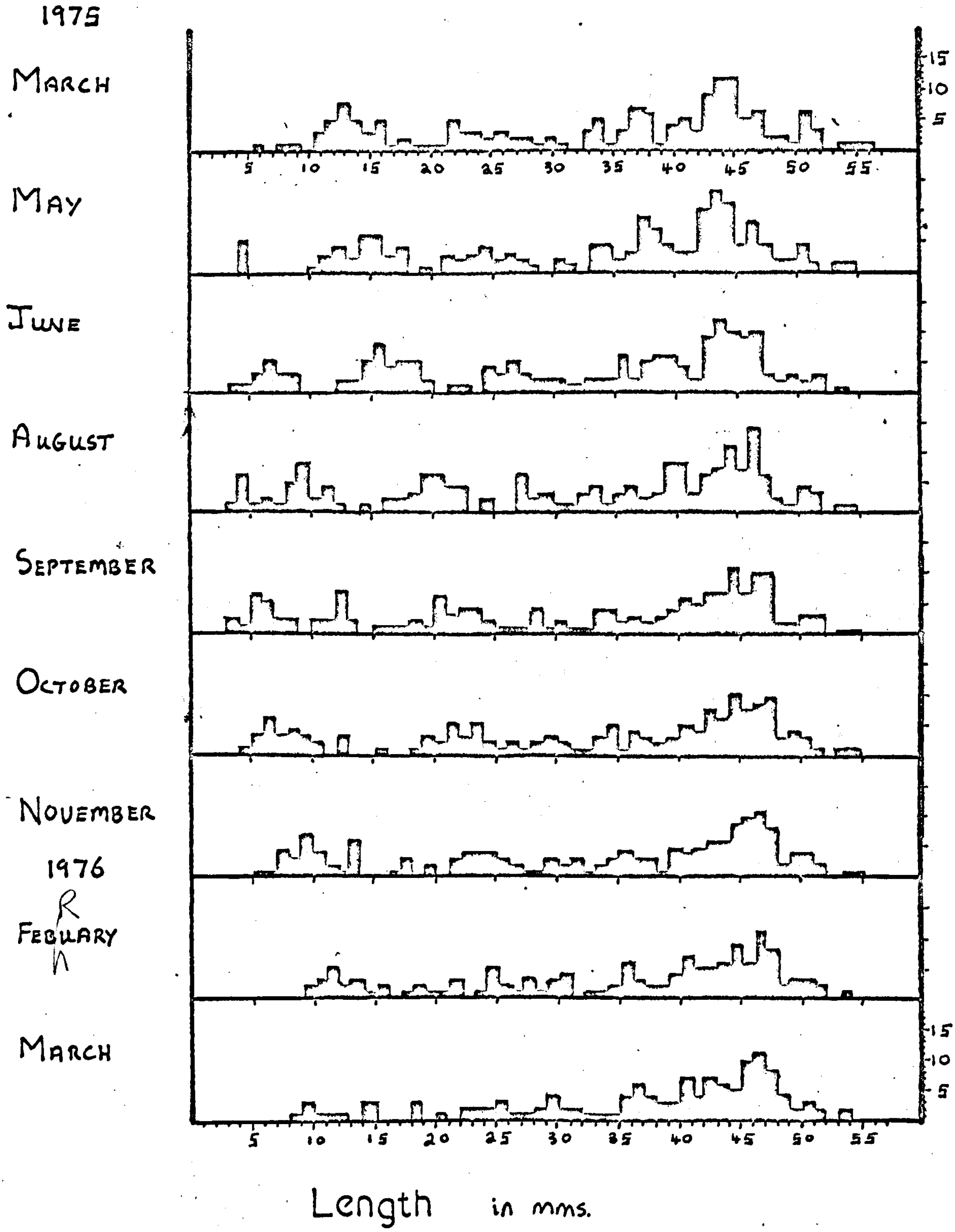


Fig. 7. The monthly length—frequency distribution of the P. vulgata quadrat population.

Fig. 8. P. vulgata: The length-frequency distribution of the quadrat population in March 1974, 1975 & 1976. The mean length (—) and the range (-----) of the year groups that were recognisable were determined.

How certain is it that annual growth increment is correct?

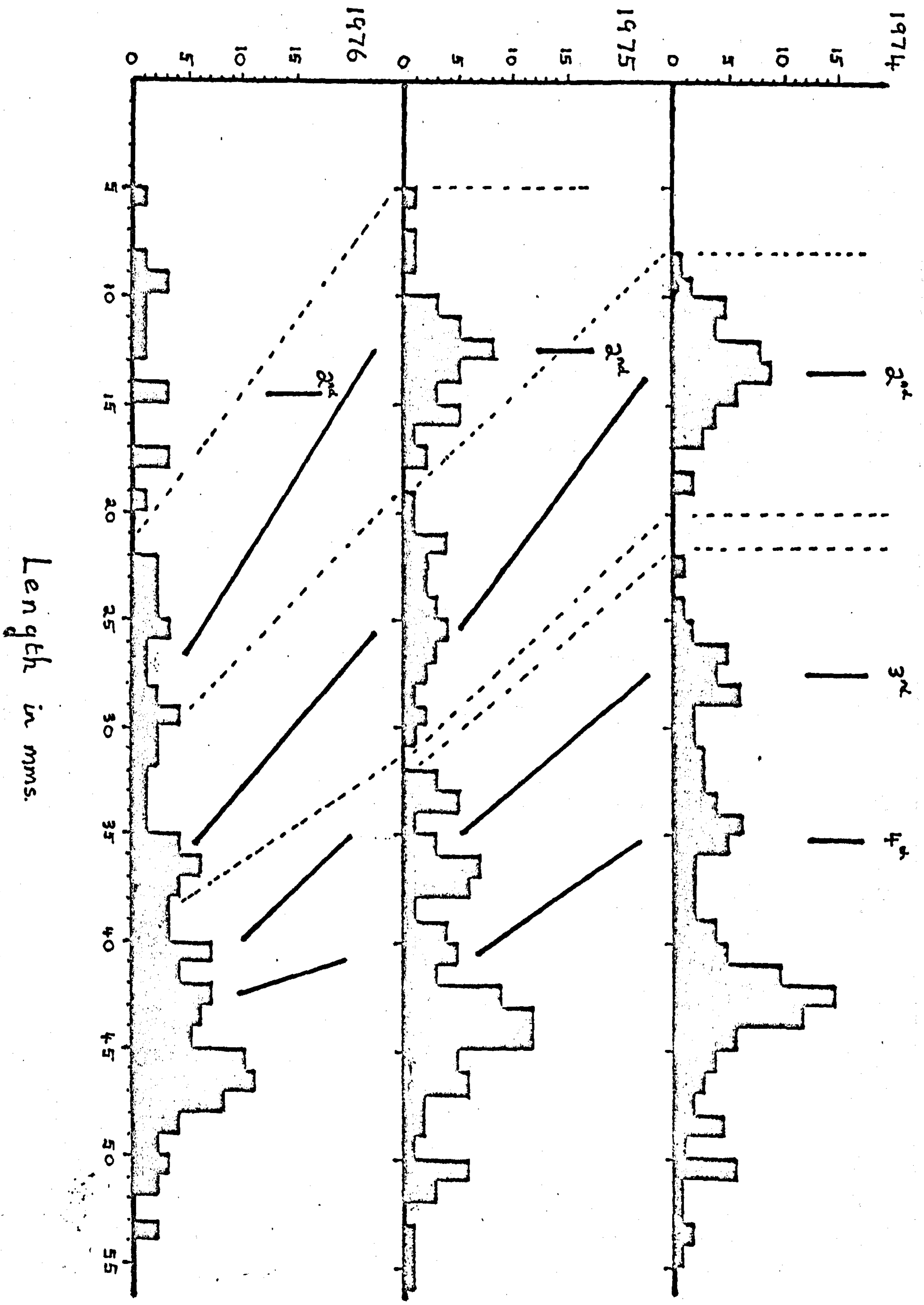


Table 1 *P. vulgata*: The average length (in mm) each month of the 1974 and 1975 spat, second, third, fourth and fifth year animals of 1974 and the maximum and minimum lengths of the spat, second and third years.

Month	1975 spat			1974 spat			Second year			Third year		Fourth year	Fifth year
	av.	min.	max.	av.	min.	max.	av.	min.	max.	av.	min.	av.	av.
1974													
March							13.00	7.94	17.80	27.00	21.9	35.00	40.00
April						4.58	14.09	8.70	18.92	27.89	23.11	35.58	40.17
May				0.16		6.23	15.40	10.03	20.18	28.71	23.96	36.35	40.40
June				1.29		8.11	17.04	10.92	21.59	29.76	25.15	36.97	40.60
July				2.88	2.64	9.96	18.18	11.29	21.69	31.15	26.32	37.70	40.87
August				4.10	3.89	11.75	19.12	16.03	23.18	31.72	27.09	38.08	40.91
September				5.54	3.39	12.65	19.85	16.79	23.92	32.03	27.36	38.36	41.02
October				6.68	4.78	13.07	20.72	17.30	24.91	32.21	27.37	38.52	41.06
November				7.90	5.14	14.03	21.80	17.36	25.70	32.38	28.22	38.68	41.09
December				8.88	4.39	14.60	22.56	16.64	25.55	32.54	28.41	38.85	41.09
1975													
January				10.02	5.08	15.65	23.48	19.21	25.70	32.92	28.54	39.16	41.12
February				11.81	5.80	16.15	24.29	18.63	26.68	33.44	29.39	39.50	41.19
March				12.40	5.00	17.43	25.00	19.08	29.77	34.15	29.39	39.78	41.27
April													
May			4.34	14.32	9.54	19.14	26.18	20.92	30.55	35.05	30.14	40.13	41.62
June			7.54	15.88	12.14	22.19	27.95	24.45	32.15	35.95	32.15	40.59	42.08
July													
August	2.52		12.18	19.36	14.45	24.42	30.29	26.52	32.99	37.30	33.78	41.08	42.57
September	5.00	3.13	12.77	20.93	15.28	25.38	31.10	27.09	34.95	37.97	33.80	41.26	42.75
October	6.34	4.45	15.47	21.52	17.65	25.73	31.69	27.32	35.46	38.16	33.74	41.35	42.84
November	9.00	5.30	16.67	22.93	18.52	26.28	32,42	27.44	35.62	38.51	34.37	41.46	42.95
December													
1976													
January													
February	12.18	8.76	20.00	24.55	20.90	28.43	33.18	27.44	36.01	38.90	34.95	41.52	43.01
March	13.53	5.45	20.13	25.77	21.70	29.29	33.93	27.77	37.80	39.48	35.90	41.64	43.13

and in 1976 was 13.53 mm ranging from 5 to 20 mm. The number of second year limpets in March was 44, 36 and 15 respectively in 1974, 1975 and 1976.

The third year animals form a discrete mode. The lower component was separate from the upper component of the second year animals but the upper component overlapped the lower component of the fourth year animals. The overlap increased as the year progressed. The average length in March 1974 was 27.00 mm ranging from approximately 33 to 22.0 mm, in 1975 was 25 mm ranging from 19 to 30 mm, and in March 1976 was 25.77 mm ranging from 22 to 29 mm. The number of third year animals in March was approximately 37, 26 and 21 respectively in 1974, 1975 and 1976.

It was not possible to graphically recognise the year classes of the quadrats' population above the third. However it was possible to follow the 1974 first, second and third year classes, and supplemented with the data on the growth rates of the quadrat limpets (discussed later) the number, mean and range of higher year classes were calculated.

The average size of the fourth year component in March 1974 was calculated as approximately 35 mm, in 1975 as 34.5 mm and in 1976 as 33.93 mm ranging from 38 to 28 mm. The number of animals in March was calculated as 37, 26 and 21 respectively in 1974, 1975 and 1976.

The average size of the fifth year component in March 1974 was approximately 40 mm, in 1975 was 39.77 mm and in 1976 was 39.48 mm with the lower limit being 36 mm. The number of animals in March 1976 was 22.

The average size of the seventh year component in March 1976 was calculated as 43.1 mm.

The largest limpet measured in the quadrats was 52.2 mm, and outside the quadrat but still on the same ledge 60.68 mm.

b. Growth analysis: The growth and average monthly growth rates for each of the identifiable year groups are shown in Tables 2 & 3 and Fig. 9.

The spat's growth in 1974 was relatively fast throughout late spring and summer reaching a maximum average of 1.44 mm a month. The growth then progressively diminished through autumn and winter, reaching a minimum monthly average rate of 0.98 mm. The 1974 spat grew an average 13.50 mm by March 1975. A similar growth pattern was observed in 1975 though a higher average monthly growth was recorded, 2.66 mm. The average monthly minimum winter value was 1.06 mm. The 1975 spat grew an average 13.53 mm by March 1976.

The second year animals' growth progressively increased through spring reaching a maximum monthly average of 1.64 in 1974. Throughout the summer the growth rate was lower, an average of 0.94 mm per month. There was a slight increase in the growth in early autumn before a progressive decrease through late autumn and winter, reaching a minimum monthly average of 0.71 mm. The pattern was similar in 1975 except that growth was higher, a yearly average growth of 13.37 mm compared to 11.99 mm in 1974. A maximum average of 1.74 mm and a minimum of 0.54 mm were recorded in 1975.

The third year animals' growth progressively increased through spring and early summer reaching a maximum monthly average of 1.39 mm. The monthly growth rate was low, an average of 0.28 mm per month, for the rest of the summer and autumn. The average monthly growth increased to an average rate of 0.54 mm in winter. A similar pattern was observed in 1975 but with a higher average yearly growth, 8.93 mm compared to 7.15 mm in 1974. The average monthly maximum was 1.58 mm, the summer and autumn average was 1.19 mm, and the winter average was 0.71 mm.

A similar growth pattern to the third year animals was observed for the fourth year animals, except that the monthly growth rates were lower. The yearly growth was 4.78 mm in 1974 and 5.33 mm in 1975.

A similar growth pattern was observed for the fourth and older year

Fig. 9. The average monthly length of the P. vulgata; 1974 spat (o—o), second (△—△), third (▽—▽), fourth (▲—▲), fifth (▼—▼), and 1975 year spat (⊙—⊙). Also the maximimum and minimum length of the 1974 spat (∘·····∘), second (▴·····▵), third (▾·····▾) and the 1975 year spat (•·····•).

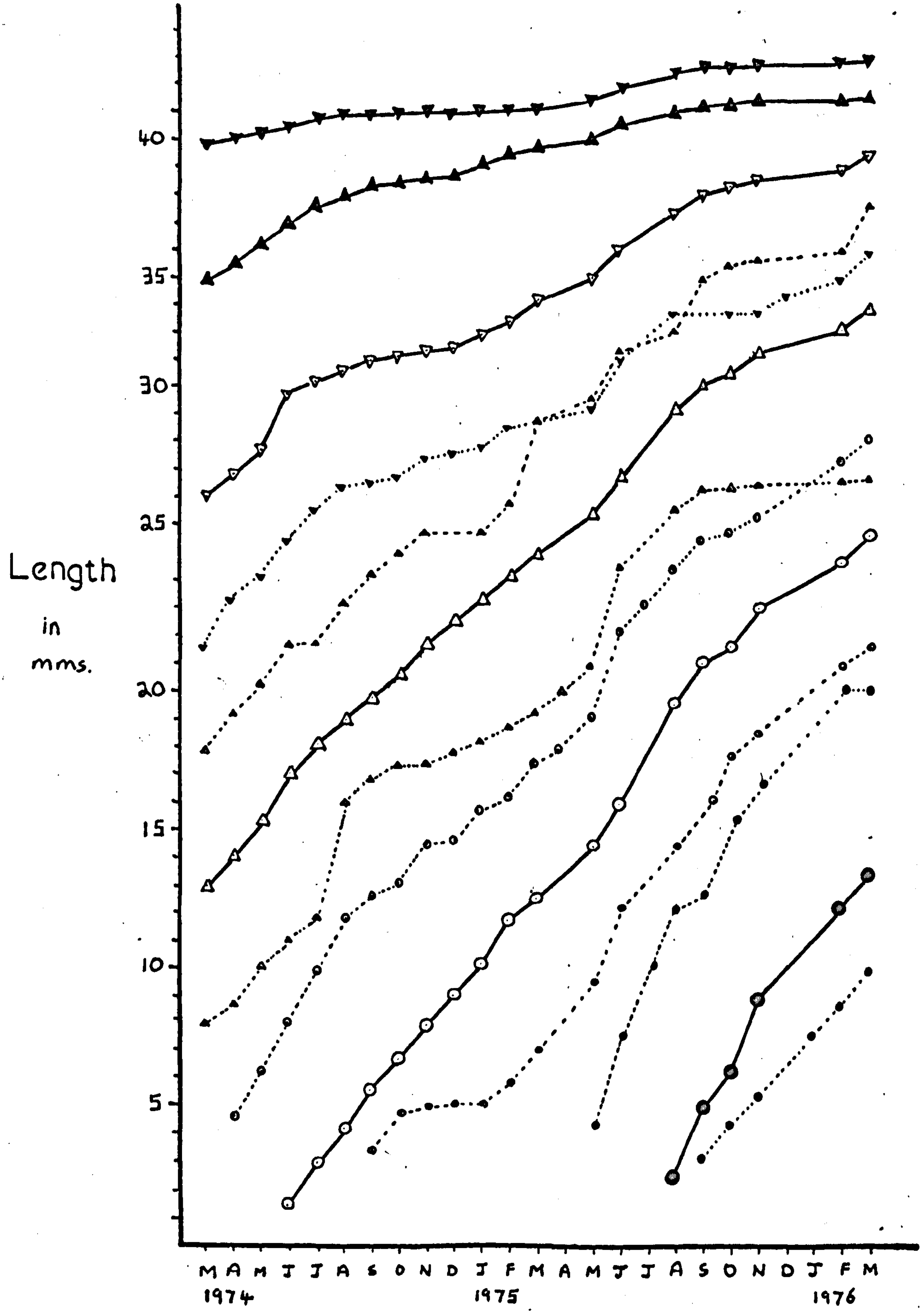

Length
in
mms.
40
35
30
25
20
15
10
5
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1974
1975
1976

Table 2 *P. vulgata*: The average growth in shell length (in mm) each month of the 1975 and 1974 spat, second, third, fourth, fifth and older animals of 1974.

Month	1975 spat	1974 spat	second	third	fourth	fifth and older
1974						
March			1.09	0.89	0.55	0.17
April		1.26	1.30	0.82	0.77	0.23
May		1.13	1.64	1.05	0.62	0.20
June		1.59	1.14	1.39	0.73	0.27
July		1.22	0.94	0.56	0.38	0.07
August		1.44	0.73	0.32	0.28	0.08
September		1.14	0.87	0.17	0.16	0.04
October		1.22	1.08	0.18	0.16	0.03
November		0.98	0.76	0.16	0.17	0.00
December		1.13	0.92	0.38	0.31	0.03
1975						
January		1.30	0.81	0.52	0.34	0.07
February		1.09	0.71	0.71	0.28	0.08
March		1.92	1.18	0.90	0.35	0.35
April						
May	1.39	1.56	1.58	0.90	0.46	0.46
June	3.09	3.48	2.53	1.35	0.49	0.49
July						
August	2.48	1.57	0.81	0.67	0.18	0.18
September	1.34	0.59	0.59	0.19	0.09	0.09
October	2.66	1.41	0.73	0.35	0.11	0.11
November	3.18	1.62	0.76	0.39	0.06	0.06
December						
1976						
January						
February	1.35	1.22	0.75	0.28	0.12	0.12

Table 3 *P. vulgata*: The annual growth in shell length and average length of the 1974 and 1975 spat, second, third, fourth, fifth year animals of 1974 in March 1974, 1975 and 1976.

Age	Average length in March (in mm)			Yearly growth (in mm)	
	1974	1975	1976	1974	1975
spat				13.50	13.53
second year	13.00	12.40	13.53	11.99	13.37
third year	27.00	24.99	25.77	7.15	8.93
fourth year	35.00	34.15	33.93	4.78	5.33
fifth year	40.00	39.77	39.48	1.27	1.85
sixth year		41.27	41.64		1.85
seventh year			43.13		

groups. the majority of the growth took place in spring and virtually none was recorded the rest of the year. The average yearly growth in 1974 was 1.27 mm and was 1.85 mm in 1975.

c. Flesh and somatic tissue regressions: The slope values of the monthly regression equations of log weight on log length were calculated for the flesh and somatic tissue (Table 4) and were plotted (Fig. 10). An increase in the slope value means an increase in the tissue weight per shell length of the limpets and a decrease vice versa. The flesh slope values increased from their low winter values, through the spring and early summer, reaching a peak in July and August in 1974 and 1975 respectively. This was followed by a decrease reaching a minimum in December in both years. The somatic tissue slope values showed a similar increase in spring and early summer but the decrease was much greater reaching a minimum in December.

d. Shell regressions: The monthly regression equations of log weight on log length calculated for the shell (Table 5) were similar giving an average value of 3.7 for the slope and -5.2337 g for the intercept.

e. Ash: The ash content of the somatic tissue was recorded as a percentage of the total dry somatic tissue weight. The percentage ash decreased from late winter to early summer, reaching a minimum of 10.74% and 10.69% in June 1974 and July 1975 respectively. This was followed by an increase reaching a peak of 13.16% and 13.06% in December 1974 and February 1976 respectively (Table 6).

f. Calorific value: The somatic tissue calorific value increased from the spring to early summer reaching a peak in July 1974 and 1975 of 4.73 and 4.24 Kcals/g respectively. This was followed by a decrease reaching a minimum of 4.45 and 4.38 Kcals/g in December 1974 and February 1976 respectively. The calorific content was also expressed as K cals per ash-free g (Table 6).

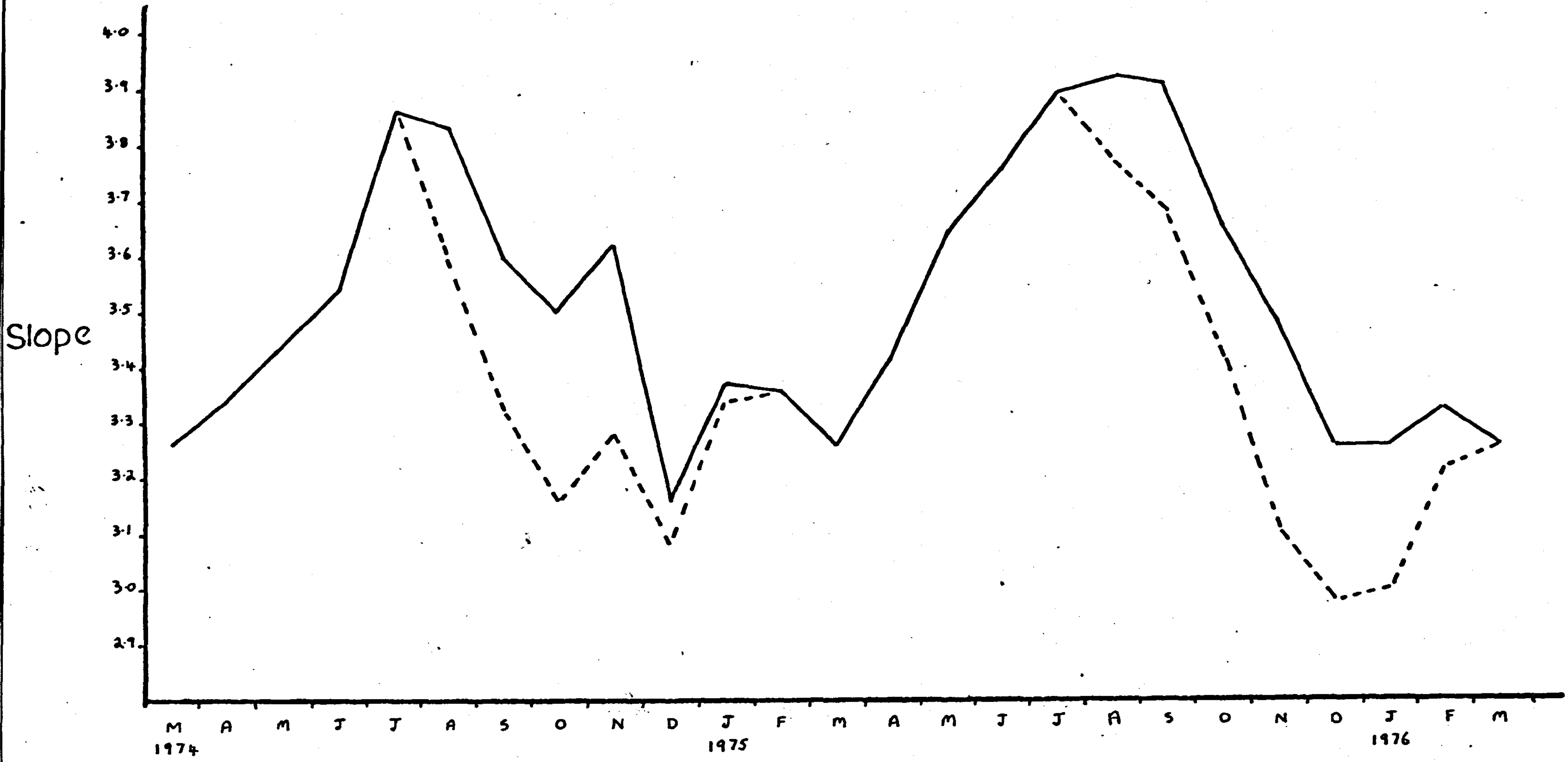


Fig.10. The monthly slope values of the log (weight–length) regression for the flesh(——) & somatic(- - - -) tissue of P. vulgata.

Table 4 *P. vulgata*: Paramaters for the regression of log flesh dry weight in g. and somatic tissue dry weight in g. on shell length in mm.

Month	correlation coefficient	Flesh intercept	Flesh slope	Somatic intercept	Somatic slope
1974					
March	99.35	-5.4957	3.2657	-5.4957	3.2657
April	99.42	-5.5501	3.3428	-5.5501	3.3428
May	98.69	-5.3434	3.2443	-5.3434	3.2443
June	99.14	-5.8635	3.5399	-5.8635	3.5399
July	99.23	-6.3433	3.8600	-5.3433	3.8600
August	98.78	-6.3146	3.8342	-6.0075	3.6197
September	99.08	-5.9998	3.6076	-5.6034	3.3307
October	97.93	-5.8498	3.5016	-5.3742	3.1615
November	98.68	-6.0226	3.6253	-5.5471	3.2852
December	98.12	-5.3822	3.1671	-5.2638	3.0897
1975					
January	98.73	-5.6702	3.3732	-5.6194	3.3366
February	97.91	-5.6547	3.3593	-5.6547	3.3593
March	97.37	-5.5295	3.2629	-5.5295	3.2629
April	98.00	-5.6921	3.4227	-5.6921	3.4227
May	98.68	-6.0019	3.6414	-6.0091	3.6414
June	92.45	-6.1618	3.7637	-6.1818	3.7337
July	96.78	-6.3828	3.8962	-6.3829	3.8962
August	97.43	-6.4320	3.9181	-6.2240	3.7830
September	97.40	-6.4273	3.9148	-6.0885	3.6856
October	97.50	-6.0049	3.6581	-5.7470	3.4281
November	96.88	-5.6347	3.3478	-5.3067	3.1132
December	98.60	-5.5082	3.2573	-5.1323	3.9834
1976					
January	97.13	-5.5057	3.2555	-5.1325	3.0017
February	98.10	-5.6039	3.3258	-5.4877	3.2207
March	98.50	-5.4685	3.2635	-5.4685	3.2635

Table 5 *P. vulgata*: Parameters for the regression of log shell weight in g. on shell length in mm.

Month	coefficient of correlation	intercept	slope
March	99.77	-5.2075	3.6846
April	99.48	-5.4277	3.8016
May	99.42	-5.9570	3.5408
June	99.62	-5.2075	3.6846
July	99.94	-5.0350	3.5811
August	99.35	-5.1485	3.6502
September	99.33	-5.4974	3.8596
October	99.22	-5.3097	3.7476
November	99.14	-5.4476	3.8340
December	99.07	-5.0579	3.5792
January	99.52	-5.1750	3.6692
February	99.44	-5.3377	3.7876
Average	99.44	-5.2337	3.7016

Table 6 *P. vulgata*: The calorific value each month of the somatic tissue.

Month	Kcals/g	S.E.	% Ash	Kcals/ash free g	S.E.
1974					
March	4.66	±0.03	11.97	5.29	±0.04
April	4.70	±0.08	11.78	5.33	±0.01
May	4.72	±0.03	10.76	5.29	±0.03
June	4.71	±0.04	10.74	5.28	±0.05
July	4.23	±0.01	10.83	5.30	±0.01
August	4.52	±0.01	11.76	5.12	±0.01
September	4.46	±0.03	11.20	5.02	±0.03
October	4.54	±0.03	11.87	5.15	±0.04
November	4.53	±0.02	12.84	5.20	±0.03
December	4.45	±0.01	13.16	5.12	±0.01
1975					
January	4.61	±0.07	11.42	5.20	±0.08
February	4.63	±0.02	11.44	5.23	±0.02
March	4.66	±0.03	11.20	5.25	±0.04
April	4.70	±0.07	10.89	5.27	±0.07
May	4.73	±0.01	10.68	5.30	±0.01
June	4.72	±0.02	10.71	5.29	±0.02
July	4.74	±0.02	10.69	5.31	±0.02
August	4.69	±0.02	10.90	5.26	±0.02
September	4.48	±0.01	11.23	5.05	±0.01
October	4.66	±0.01	11.58	5.28	±0.02
November	4.53	±0.08	11.87	5.14	±0.09
December	4.52	±0.08	12.20	5.15	±0.09
1976					
January	4.52	±0.08	11.90	5.13	±0.09
February	4.38	±0.02	13.06	5.04	±0.02
March	4.66	±0.02	11.51	5.27	±0.02

g. Somatic tissue energy content: The energy content of the somatic tissue of the quadrats increased from 299 Kcals in March 1974 reaching a peak of 457 Kcals in July which was followed by a rapid decrease to 282 Kcals in September followed by a slower decrease until December, when a minimum of 233 Kcals was recorded. The somatic tissue calorific value then once more increased reaching a peak of 453 Kcals in July 1975, which was followed again by a rapid decrease reaching a minimum of 216 Kcals in December and then increased to 305 Kcals in March 1976. The average somatic tissue calorific value was 324 and 329 Kcals in 1974 and 1975 respectively (Table 7 and Fig. 11).

h. Flesh energy content: The energy content of the flesh tissue of the quadrats increased from 350 Kcals in March 1974 reaching a peak of 518 Kcals in July, which was followed by a sharp decrease to 389 Kcals in September, followed by an increase to 412 Kcals in November, followed by a further decrease reaching a minimum of 315 Kcals in December. The value increased again, except for a slight decrease in March, reaching a peak of 516 Kcals in August 1975, which was again followed by a decrease reaching a minimum of 312 Kcals in January and then increased to 355 Kcals in March. The average calorific value was 404.7 and 424.5 Kcals in 1974 and 1975 respectively (Table 7 and Fig. 11).

i. Mortality: Two survival curves (Fig. 12) were constructed using the numbers of each year group recorded in March 1974, 1975 and 1976. Mortality is assumed to take place from first settlement; however changes in juvenile numbers only reflect the balance between recruitment and death, and the situation is further complicated by the extent and timing of the supplementary emergence and immigration. Consequently the mortality for the first few months cannot be calculated. However once settlement and immigration were completed mortality was calculated. The mortality rate for late autumn and winter in 1974 was 10% per month, and 12% per month in

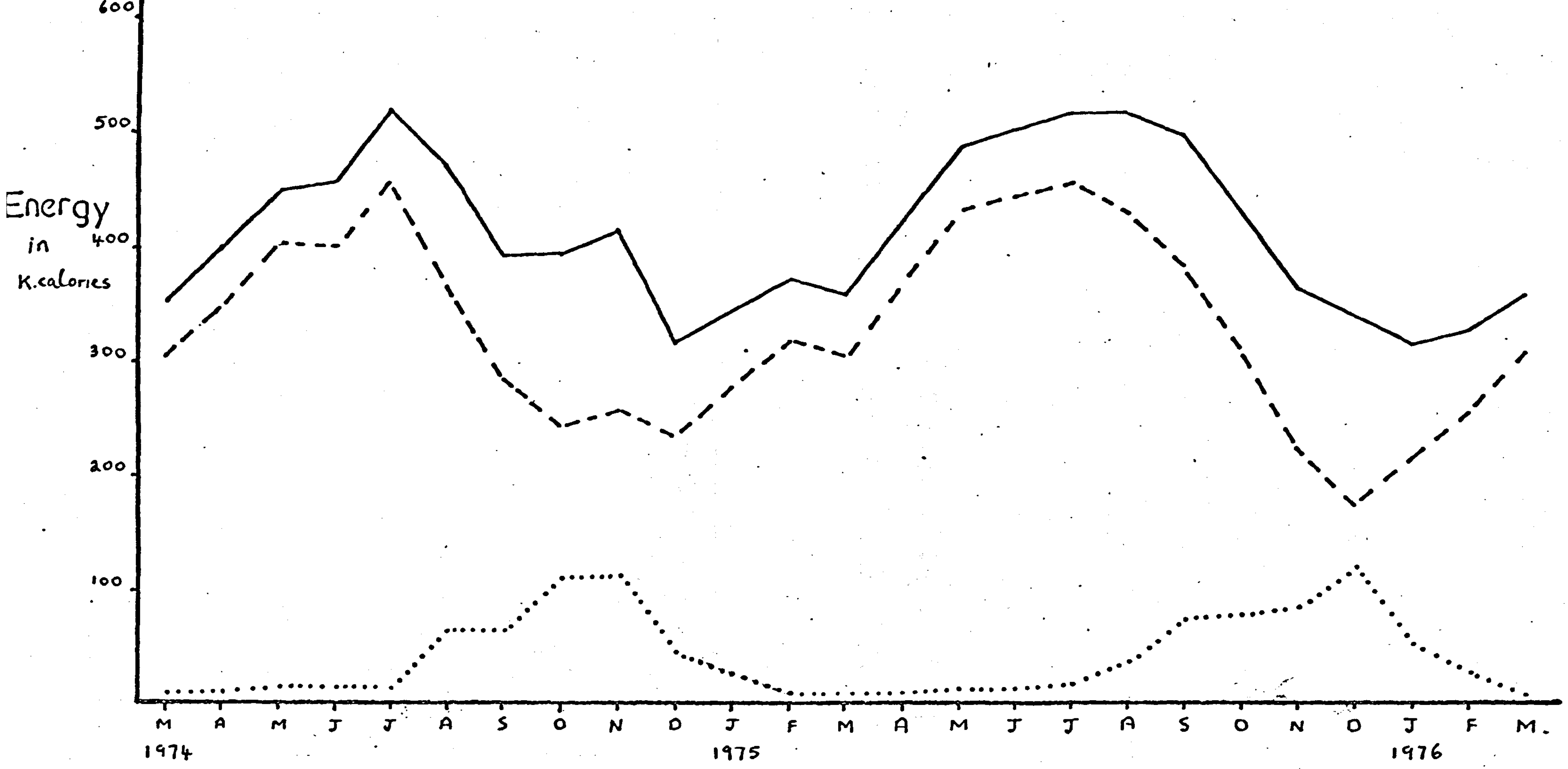


Fig. II. The monthly energy content of the somatic tissue, gonad and biomass of the P. vulgata population. Biomass (——), somatic (- - -) & gonadal (·····).

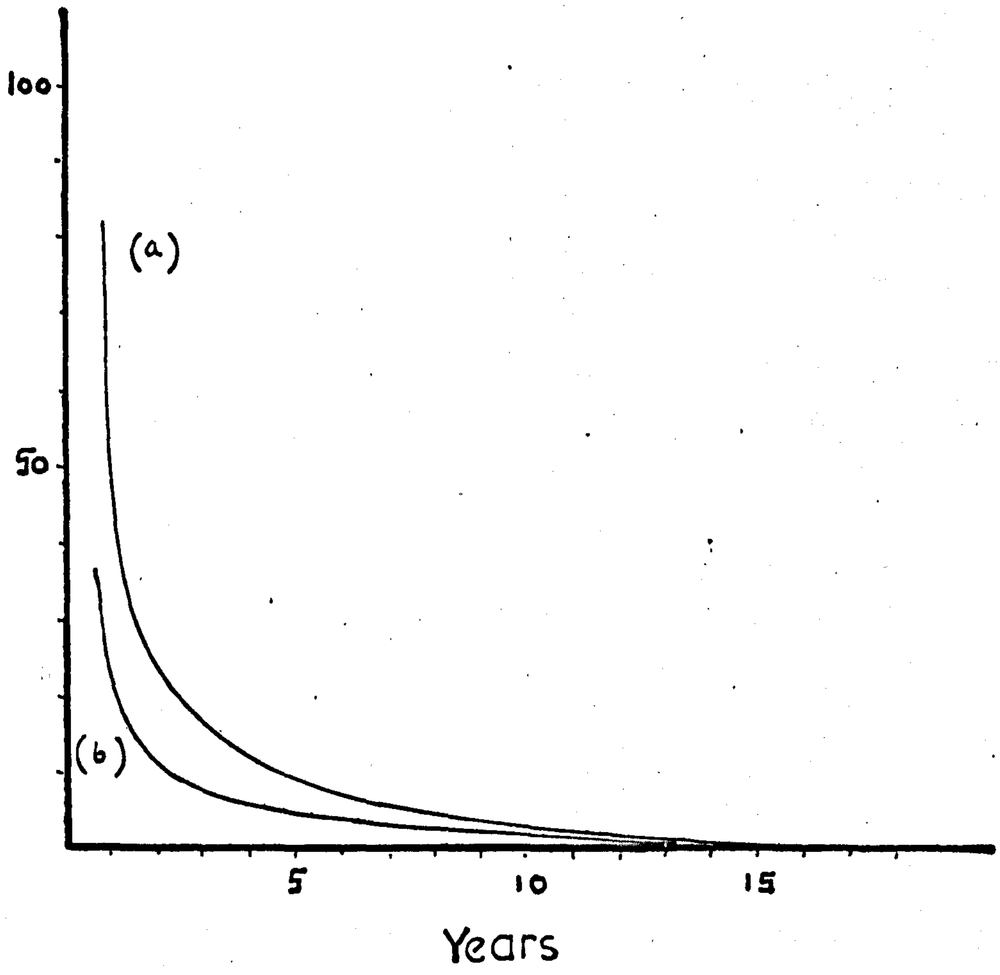


Fig. 12. P.vulgata survival curves for 1974 (a) and 1975 (b).

<u>Table 7</u> *P. vulgata*: The number, calorific value of the somatic tissue, gonad tissue, shell and biomass of the quadrats' population.

Month	Number	Somatic (Kcals)	Gonadal (Kcals)	Shell (Kcals)	Biomass (Kcals)
1974					
March	168	299.2	10.1	40.3	349.6
April	172	345.5	12.2	40.9	398.6
May	171	399.7	13.9	42.4	447.2
June	177	397.6	13.9	42.5	454.0
July	189	457.3	16.6	44.2	518.1
August	232	361.6	65.0	44.1	470.7
September	232	282.2	64.4	42.7	389.3
October	213	241.5	110.0	42.3	393.8
November	214	255.5	113.9	42.6	412.0
December	178	232.5	43.1	39.2	314.8
1975					
January	177	276.4	23.2	39.9	339.4
February	161	317.7	22.4	39.7	368.7
March	160	303.7	10.2	40.3	354.2
April	160	367.0	12.0	41.0	420.0
May	160	429.0	15.3	41.8	486.6
June	174	443.2	16.7	42.5	502.4
July	175	453.6	18.1	43.5	515.2
August	176	431.0	40.7	44.4	516.1
September	166	379.0	73.4	43.9	496.3
October	154	310.7	78.5	42.8	432.0
November	156	224.5	85.5	41.3	359.7
December	149	176.3	119.5	40.6	336.4
1976					
January	142	215.5	57.0	39.9	312.4
February	136	254.8	29.4	39.3	323.5
March	130	304.5	10.2	40.4	355.1

1975. The second year mortality was 41% in 1974 and 42% in 1975. The average mortality rate for the fourth and third years was 23%. The mortality for older animals was also 23% (Table 8). The mortality varied monthly from a maximum of 23 to -4 Kcals. The overall yearly mortality was 65.7 and 93.5 Kcals in 1974 and 1975 respectively (Table 9).

j. Production: The growth production (somatic tissue and shell) each month was the difference between that month's somatic tissue and shell energy content of the quadrats and the following month's (Table 7) plus the energy content of the somatic tissue and shell of that month's mortality (Table 9). Each month's growth production was added to give the yearly production (P_g) which was 39.3 Kcals and 94.4 Kcals in 1974 and 1975 respectively (Table 9). The seasonal changes in growth production are shown in Fig. 13.

Discussion

The minimum spat size observed in the quadrats was 2.44 mm. Smith (1935) observed spat to first settle on the shore at a size of 0.2 mm, while Jones (1948) at Port St. Mary found spat at the beginning of February at a size of 0.75 mm. Jones observed that spat settled in shallow pools and then showed a tendency to move out on reaching a size of 3 mm and to colonize the dry rock. The quadrats contained no pools, only small shallow water-filled hollows. Therefore it is very likely that the spat are settling in nearby pools and not colonizing the quadrats until they have reached a size of 3 mm or more. The time of spat settlement depended on the time the gametes were released by the adults. The gametes are usually released between November and the end of February, varying from year to year (see reproductive chapter). In 1974 mid spawning was during December, but the next was not until early January 1976. Thus the spat were likely to have settled by the beginning of January in 1975 and at the end of January in 1976, as the free swimming larva is limited to two weeks (Smith 1935 and Dodd 1957). The average spat size in July 1974 was 2.9 mm and 2.50 mm in August 1975.

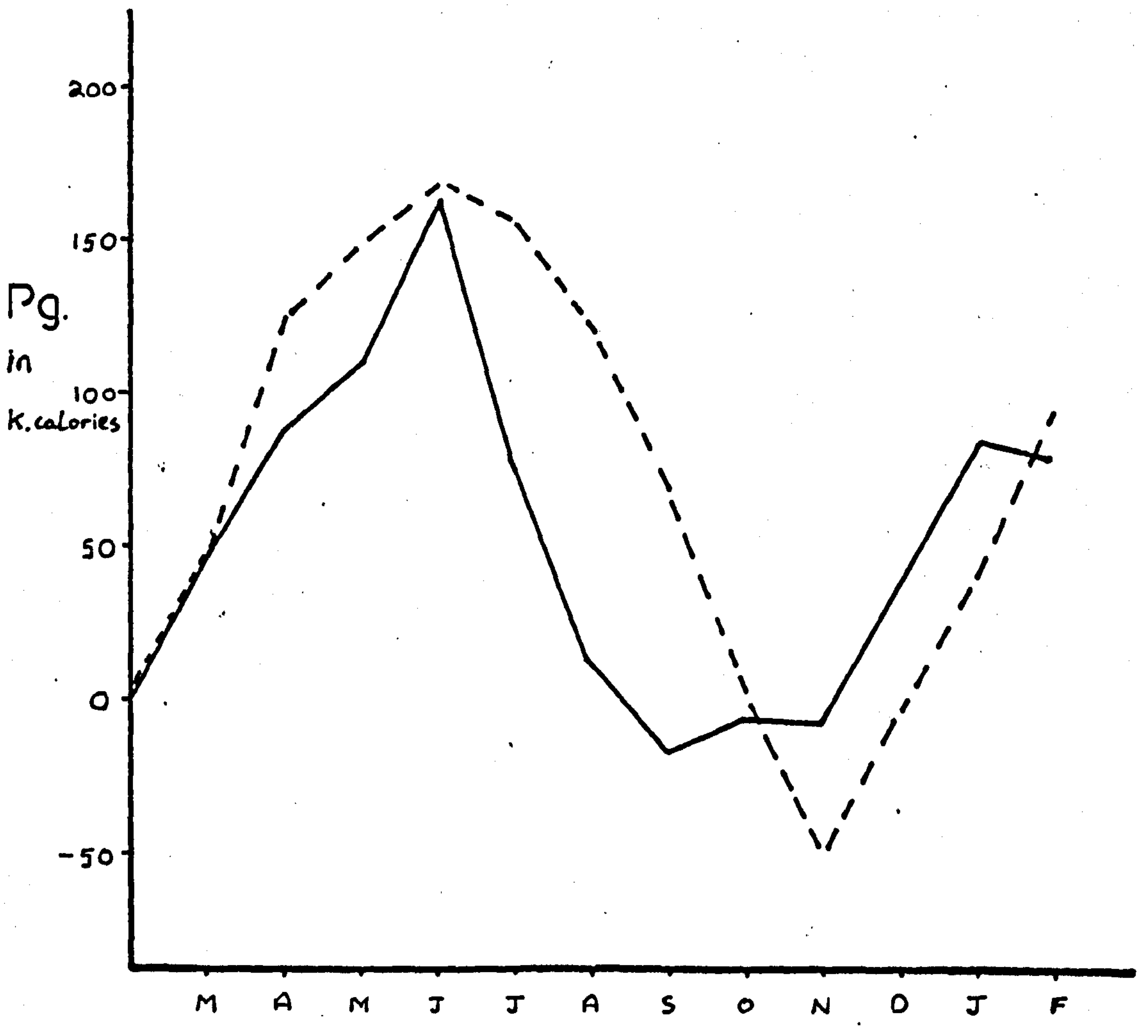


Fig. 13. The changes in growth production (Pg.) in 1974 and 1975 for the P. vulgata population. 1974 (——) & 1975 (- - -).

Table 8 *P. vulgata*: The annual mortality (as a percentage) and age distribution.

Age	Number of animals present					Mortality			
	March 1974	Sept.	March 1975	Nov.	March 1976	1974	Sept. to March	1975	Nov. to March
spat		97		29			63		48
second	44		36		15	41		42	
third	37		26		21	22		23	
fourth			29		20			24	
fifth					22				
older animals	87		69		52	21		25	

Table 9 *P. vulgata*: The growth and mortality of the somatic tissue and shell of the quadrats' population.

Month	Growth			Mortality		
	Somatic (Kcals)	Shell (Kcals)	Total (Kcals)	Somatic (Kcals)	Shell (Kcals)	Total (Kcals)
1974						
March	46.2	0.9	47.2	0.0	0.3	0.3
April	50.2	1.1	51.3	-4.0	-0.4	-4.4
May	9.6	1.3	10.8	11.7	1.2	12.9
June	55.5	1.5	57.1	-4.1	-0.2	-4.3
July	-86.2	0.7	-85.5	9.5	0.8	10.3
August	-66.2	0.0	-66.1	13.2	1.4	14.6
September	-32.1	0.7	-31.4	8.7	1.1	9.8
October	11.7	0.0	12.3	-2.4	-.03	-2.7
November	-2.8	0.3	-2.5	20.2	3.2	23.4
December	45.6	0.6	46.2	1.7	0.4	2.1
1975						
January	46.4	0.5	46.8	5.0	0.7	5.7
February	-16.5	0.3	-16.2	-2.5	-0.3	-2.8
March	122.2	2.0	124.2	-3.6	0.5	-3.1
April						
May	23.9	1.7	25.5	10.1	1.0	11.1
June	4.4	3.6	8.0	16.4	1.7	18.1
July						
August	-35.1	1.1	-34.0	16.9	1.6	18.5
September	-53.6	0.3	-53.0	15.2	1.4	16.6
October	-64.7	0.3	-64.4	12.1	1.3	13.4
November	33.1	0.5	33.6	11.6	3.0	14.6
December						
1976						
January						
February	53.2	1.6	54.8	3.5	0.5	4.0

Thus the growth is relatively slow for the first six months, being at a rate of 0.48 mm / month in 1974 and 0.42 mm / month in 1975. When the animals reached a size of approximately 3 mm the growth rate rapidly increased up to 1.59 mm / month in 1974 and 2.66 mm / month in 1975. Blackmore (1969) at Robin Hood's Bay observed a similar pattern of growth. In 1965 he observed a rate of 0.4 mm / month and 0.55 mm / month in 1966 for the first six months. This was followed by a marked increase, up to 2.0 mm in 1965 and 1.28 mm / month in 1966. This high growth was maintained until early autumn when the rate slowly and progressively diminished until spring when the rate increased.

The growth rate for all the year groups progressively increased from early spring to early summer. The growth rate for the second and third year animals was depressed over the summer and autumn but increased in mid-winter, while the growth rate of older animals more or less ceased over the summer and autumn but increased in mid-winter. This pattern suggests that the growth was influenced by temperature and gonad development.

Temperature probably influenced the spat's and the older animals' growth during mid-winter, spring and early summer. The growth rate was observed to progressively increase with the rise in sea temperature encountered from spring to early summer. The growth rate, except for the spat, was depressed in the summer and early autumn when the sea reached its maximum temperature. This reduction in growth rate in early summer and continued depression until mid-winter was probably due to gonadal development. Gonadal development commences in July and continues until spawning takes place which was in December and January. Ripe gonads of fourth year and older animals comprised between 24 and 27% of the flesh weight. Thus it is not surprising that growth virtually ceased as the energy required for growth would have been channelled for the gonad development. The growth rate of third year animals was depressed during the summer but still relatively high. Though the gonads of these animals developed, their relative size compared to older animals was much smaller, e.g. ripe gonads were 52% smaller. The growth rate of the second year animals was only slightly reduced. Though these animals did not produce ripe gonads, some development especially in the larger animals was observed. The spat showed no sign of any gonadal development and their growth rate increased throughout the summer and progressively decreased through the autumn and winter. This decreasing growth rate corresponded to the fall in sea temperature at this time of year. It was noticed that as soon as spawning had commenced in mid-winter the growth rate increased in the older animals.

This temperature influence explains the fact that growth was greater in 1975 than in 1974 as the average monthly temperature in 1975 was higher than in 1974.

The yearly growth diminished with age. The spat grew approximately 13.50 mm, the second year animals 11.99 to 13.37 mm, the third year 7.15 to 8.93 mm, the fourth 4.28 to 5.33 mm and the fifth and older animals 1.27 to 1.85 mm. As observed by the other workers, P. vulgata continues growing throughout life.

The mortality rate was observed to decrease with age (Fig. 9, and Table 8). The monthly spat mortality in the autumn and winter was 10 - 12%. Lewis and Bowman (1975) calculated a 78 to 86% loss of spat from August to the end of the year which is a slightly higher mortality, 17 to 16% per month, than observed in this study. The second year mortality is 41 to 42%. The mortality rate for the older animals was seen to vary from 21 to 25% giving an average of 23%.

The survival curves derived from these mortality rates are very similar to those constructed by Lewis and Bowman (1975). It was estimated from the curves that the maximum life span for the limpets in the quadrats is 12 to 15 years. The maximum size of an animal in the quadrats was 55.20 mm. If its growth was average this animal was 13 years old. The maximum size of an animal found on the ledge was 60.68 mm and it was calculated to be 17 years old. These maximum ages compare with Hatton (1938) and Fischer-Piette (1939, 1941, 1948) who estimated that P. vulgata at their locations lived up to 16 years, while Lewis and Bowman (1975) calculated that they lived up to 15 to 17 years at Robin Hood's Bay.

If the plots of monthly biomass and somatic tissue (Fig. 11) are compared with the plot of monthly slope of the regression equations (Fig. 10) the overall pattern is seen to be very similar. An increase in the slope value means an increase in the tissue weight per shell length of the limpets and a decrease vice versa. Thus the changes in the biomass and somatic weights were mainly changes in weight per shell length. Growth in length and the associated increase in weight will also affect the biomass and somatic tissue. However over the two years this was negligible as this increase in weight was counteracted by mortality. Though the increases in weight due to length growth and mortality differ from month to month over the year they were approximately equal. In 1974 growth production was 69.3 Kcals while mortality was 64.7 Kcals, and in 1975 growth was 94.4 Kcals while mortality was 93.5 Kcals. Any change in the calorific value of the tissues will have affected the monthly biomass and somatic tissue (Table 6). These changes were correlated with the weight per shell length changes of the animals and are discussed later.

The biomass (Table 7 and Fig. 11) in 1974 increased during the spring and early summer, from 349.6 Kcals in March to a peak of 518.1 Kcals in July, and then decreased from July to December reaching a minimum of 314.8 Kcals. The biomass then increased reaching a peak in August 1975 of 516.1 Kcals, before again decreasing reaching a minimum of 312.4 Kcals in December. The biomass then increased reaching 355.1 Kcals by March 1976. Blackmore's (1969) observations at Robin Hood's Bay were similar to this study, that during the early months of the year, January to April, the dry weight was minimal, but increased rapidly during May to August as the temperature increased and the food supply became abundant. During this period in the study the calorific content increased by two-thirds compared to a doubling in weight recorded by Blackmore (1969). Blackmore (1969) then observed that the dry weight decreased reaching a minimum value in January.

The biomass consists of the somatic tissue gonad and shell. The shell calorific content was small compared to that of the somatic tissue and gonad, so the latter two had the major influence on the biomass content. The somatic tissue calorific content increased during the spring and early summer, from 299.2 Kcals in March 1974 to a peak of 457.3 Kcals in July. In 1975 the increase was from 303.7 Kcals to 453.6 Kcals. This was followed by a decrease in calorific content reaching a minimum of 232.5 Kcals in December 1974 and 176.3 Kcals in December 1975. This summer peak and corresponding decrease in somatic tissue calorific content correspond to the development of the gonads. In 1974 the gonads began developing in July, became ripe in November and spawning commenced in December.

Blackmore (1969) observed that the levels of polysaccharide and lipid components of P. vulgata varied with season. During the spring and early summer the polysaccharide (largely glycogen) content of the somatic tissue showed a marked increase which continued until July when a peak value of about five times the winter level was attained. The content then decreased reaching a minimum in December. This peak corresponded to the onset of gonad development. In the male limpets this decrease was associated with a corresponding increase within the testes. The increase of polysaccharide within the ovary during maturation was, however, significantly less than in the testes. Two of the main glycogen storage tissues are the foot and hepatopancreas, and Barry and Munday (1959) observed that there is a rapid increase in glycogen in these tissues from April to July to five times the winter content, followed by a decrease during gonad development until the content is practically negligible in December.

Blackmore (1969) observed that the lipid content of the somatic tissue was at a minimum in winter and increased during spring and early summer, reaching a peak in August.- During maturation lipid accumulated in the gonad and at the same time the level in the somatic began to fall. The lipid level in the ovary was significantly higher than in the testes.

The immature (spat and second year) animals did not show any obvious seasonal trend in calorific content of the biomass or somatic tissue. Blackmore (1969) found that, unlike the mature limpets, the virgin immature animals did not show any obvious seasonal trend in polysaccharide and lipid content.

This decrease in food reserves within the somatic tissue observed by Blackmore (1969) and the loss in the calorific content during the summer may be attributed to the developing gonad. Gonad development involves intense biochemical synthesis, with the formation of large amounts of nucleic acids for the spermatozoa and much lipid and protein for ova. Whether, in Patella, the gonad utilizes the reserves, or whether the diversion of immediately absorbed food to the gonad necessitates the utilization of the food reserves by itself cannot be stated, but since the accumulation of reserves within the gonads more or less parallels the depletion of reserves within the somatic tissue it seems reasonable to attribute this to their transfer.

The calorific values of somatic tissue (Table 3) were seen to increase from 4.66 Kcals/g in March 1974 to a peak of 4.73 Kcals/g in July. The value then decreased reaching a minimum of 4.45 Kcals/g in December. In 1973 the peak was reached again in July and was 4.74 Kcals/g, while the minimum of 4.38 Kcals/g was reached in February 1976. The increase in calorific value was associated with a corresponding increase in the glycogen and lipid content of the somatic tissues. Lipids have a calorific value of 9.45 Kcals/g, proteins 5.65 Kcals/g and carbohydrates 4.20 Kcals/g. Thus the build-up of the lipid stores would produce the rise in calorific value and vice versa. The ovaries' calorific value increased with the corresponding increase in lipid content from 4.69 Kcals/g at the resting stage to

6.04 Kcals/g when ripe (stage V) (Table 15), while the testes only increased from 4.69 Kcals/g to 4.73 Kcals/g when ripe. This was because the lipid content of the ovaries was much higher than the testes, while the testes had a much higher polysaccharide content.

Barry and Munday (1959) suggested that their biochemical observations led to the conclusion that Patella does not feed during the winter and may pass into an inactive state comparable to the hibernation of terrestrial molluscs. However Blackmore (1969) concluded from his analysis that there was no 'hibernation'. The observations of this study conclude that there was no hibernation as the somatic tissue calorific content progressively increased from January in 1974 and 1975. This was only possible if the animals were feeding. Patella may not feed during spawning as in 1974 there was a loss in somatic tissue calorific content during the month preceding commencement of spawning, but this was not apparent in 1975.

The animals feed during gonad maturation as limpets were observed foraging in the middle of September (Hartnoll and Wright, in press). Also during the month between ripening (stage V) and spawning in 1974, when there will have been little energy requirement by the gonads, the somatic tissue calorific content increased. This was only possible if the animals were feeding.

Whereas the biomass or somatic tissue calorific content does not necessarily indicate growth in length, shell content does. An increase in the shell calorific content of an animal is associated with an increase in length. The shell calorific content progressively increased in the spring and early summer. In March 1974 the monthly increase was 0.9 Kcals which increased, reaching a peak of 1.5 Kcals in June. The monthly increase was diminished in July to 0.7 Kcals, while during the summer and autumn the increase was further diminished to approximately 0.25 Kcals / month. The pattern was similar in 1975 except that the increase continued until it reached 1.8 Kcals in July, decreased to 1.1 Kcals in August, and was further diminished to 0.2 Kcals / month for the rest of the summer and autumn until February 1976. This corresponds to the measured increase in length, with sea temperature influencing growth in the spring and early summer, i.e. the growth increasing with increasing temperature, and the diminished growth in summer and autumn corresponding with gonadal development.

The mortality was 64.7 Kcals in 1974 and 93.5 Kcals in 1975, while the growth was 69.3 Kcals in 1974 and 94.4 Kcals in 1975. The growth in 1974 was 4.6 Kcals greater than the mortality, so the biomass for the quadrat area increased by this amount from 349.6 Kcals to 354.2 Kcals (a 1% increase in biomass). In 1975 the biomass increased by 0.9 Kcals to 355.1 Kcals (a 0.25% increase in biomass). However the growth and mortality in 1975 were 27% greater than in 1974. The increased growth will have been due to the higher sea temperature of 1975 compared to 1974, and also because the high growth rate continued for a month longer in the summer, until August in 1975 but only until July in 1974. The Patella population of the quadrats was stable as the mortality and growth were approximately equal, and the biomass remained fairly constant during the study period. The optimum population in March for the quadrats must have been approximately 355 Kcals (i.e. 71 Kcals/m^2).

3. Littorina littoralis

Introduction

L. littoralis has no recognisable growth rings in its shell and therefore growth was measured by observing individual specimens over a period of time and determining the increase in shell length (from apex to aperture).

None of the previous workers has measured growth, except for Guiterman (1970) who followed growth over a six month period in the laboratory and for much shorter periods in the field at the Menai Straits and Fowey estuary.

The littorinids move freely over algal fronds and the rock surface especially when damp. Little movement is possible on fine-grained, mobile material such as sand or mud. Despite the relatively small excursions made by the littorinids, the majority remain in one location only for approximately five days (Bray 1974). Tidal movements are responsible for the transportation of the animals, usually carrying them a considerable distance.

The Fucaceae are generally accepted as the food source for L. littoralis (Barkmann 1955 and Guiterman 1970). In order that the growth rate of the littorinids can be measured in the field the animals must be enclosed on the algae to prevent water movements carrying them away.

Material and methods

For the field studies of growth large fucoid plants, three each of Fucus serratus and Fucus vesiculosus, were enclosed in individual bags of 5 mm knotless plastic mesh. The use of a smaller mesh caused the algae to start decaying after a few weeks. Twenty to thirty of the specimens on each plant were marked with waterproof paint, selecting only specimens of 8 mm shell length or greater since smaller individuals could pass through the mesh. The animals were measured approximately every two weeks, and the study was continued for eighteen months.

Studies were also made in the laboratory, but were complicated by the tendency of the animals to climb the sides of the aquarium under the influence of strong negative geotaxis. Even when escape was made impossible the animals remained at the highest level in the aquarium. Further difficulty was experienced with the fucoid plants, which rapidly decayed when in contact with the bottom of the tank for a few days. These problems were overcome by keeping the animals on algal fucoids which floated freely in the aquarium away from the sides. Four aquarians were set up, two with F. serratus and two with F. vesiculosus, and maintained at the ambient field temperatures. Ten to twenty animals between 3 and 8 mm were marked with waterproof paint and placed on the floating fucoid in each aquarium. The animals were measured every fortnight and the fucoid changed each month. Animals over 8 - 10 mm became sluggish after a few weeks and their growth rate was much lower than that measured in the field, so animals over 8 mm were excluded. The field and laboratory experiments covered complementary size ranges.

Each month ten 100 g dry weight samples of F. serratus and F. vesiculosus were collected at random from the same ten locations on the study ledge (Fig. 5) and the shell lengths of all the animals measured. Each month thirty of the littorinids from the twenty samples collected were dropped for a few seconds in boiling water and the flesh removed whole using a bent pin. The flesh was dry weighed, part was used to determine ash content and part to determine calorific value using the Phillipson micro-bomb calorimeter. The shell length and weight of the animals were measured. Regressions of log shell weight and log flesh weight against log shell length were calculated. The lengths of all the littorinids of the monthly sample were substituted in the regression equations and their shell and flesh weights obtained. The calorific value of the flesh was derived using the conversion factor determined previously, and the shell calorific value using the same conversion factor (0.0627 Kcals/g) that was used for Patella vulgata.

Results

During the first year shell growth rate increased from January (0.32 mm / month) until August (1.65 mm / month) and then decreased. The animals grew on average 10.45 mm in the first year. The growth of the second year animals showed a similar pattern, increasing from 0.18 mm/month in January to 0.82 mm/month in August before decreasing. The second year shell growth was on average 4.61 mm (Table 10). No shell growth was observed for the third year animals.

The density of the animals per kilogram dry fucoid was similar in each month, and no seasonal pattern was observed. F. vesiculosus supported

Table 10 *L. littoralis*: The average monthly shell growth of the juveniles.

	Shell growth (mm)	
	First year	Second year
January	0.32	0.18
February	0.40	0.19
March	0.42	0.29
April	0.26	0.27
May	0.66	0.56
June	1.24	0.44
July	1.68	0.87
August	1.75	0.82
September	1.24	0.31
October	0.88	0.29
November	0.76	0.22
December	0.84	0.17
Total	10.45	4.61

a higher number of mature (15 to 17 mm) and newly hatched littorinids than *F. serratus*, while the latter supported a larger number of middle-sized animals (6 to 12 mm) (Table 11).

The combined number of littorinids per kilogram dry weight of fucoid (Table 11) showed a high number of small animals decreasing in abundance with increasing length up to 11 mm when the abundance increased reaching a peak at 15 mm before decreasing. The maximum shell length recorded was 17.01 mm.

The regression equations calculated each month of flesh and shell weight against length were very similar. The average coefficient of correlation, intercept and slope of the regressions of log flesh weight on log length were 99.92, -5.0692 and 3.2893 respectively, and for the regressions of log shell weight on log length were 99.89, -3.3861 and 2.8984.

The calorific value and ash content of the flesh remained constant throughout the year. The calorific value of the littorinid flesh was 4.83 ± 0.11 Kcals/g or 5.33 ± 0.12 Kcals/ash free g, and the ash content was 9.42%. Thus the average calorific content of the littorinids per dry kilogram of fucoid was 23.98 Kcals (Table 11).

The mortality was determined separately for the first and second year juveniles, and adults. The first year littorinids were separated into millimetre size classes (Table 12) and their frequency determined. The mortality was determined between each millimetre group (e.g. between 1mm and 2 mm the mortality was 714-355 = 359), and it was assumed that the weight of the mortality was equivalent to all the individuals being eliminated at a weight halfway between each millimetre group. This gave a mortality of 1.06 Kcals (Table 12). This was the mortality of all the first year animals growing one millimetre on average. The animals grew eleven millimetres in their first year so the annual mortality was 11.66 Kcals (11 x 1.06 Kcals).

The first year juveniles enter their second year when reaching a size

Table 11 *L. littoralis*: The length-frequency of the littorinids per kilogram dry weight of *F. serratus*, *F. vesiculosus* and the fucoids combined. Also the calorific value of the flesh and shell of the littorinids per kilogram dry weight of the fucoids combined.

Length (mm)*	Number of animals per Kg dry weight			Calorific value of flesh (Kcals)	Calorific value of shell (Kcals)
	F.serratus	F.versiculosus	Combined		
1	473	955	714	0.0290	0.0184
2	228	482	355	0.1425	0.0682
3	57	107	88	0.1333	0.0548
4	15	31	23	0.0903	0.0330
5	14	14	14	0.1145	0.0383
6	9.1	6.9	8	0.1193	0.0371
7	8.8	6.6	7.7	0.1908	0.0559
8	9.4	8.2	8.8	0.3386	0.0940
9	8.4	5.6	7.0	0.3965	0.1052
10	8.1	3.9	6.0	0.4806	0.1224
11	11.8	10.2	11.0	1.2065	0.2244
12	16.1	7.3	11.7	1.7084	0.4048
13	9.8	10.2	10.0	1.9001	0.4363
14	10.9	16.1	13.0	3.1525	0.7031
15	19.6	28.0	23.8	7.2421	1.5722
16	4.9	6.1	5.5	2.0692	0.4381
17	0.5	0.5	0.5	0.2294	0.0475
			Total	19.5252	4.5226

* The limits of the millimetre lengths are for 1 mm, 0.5 to 1.49 mm, 2 mm, 1.50 to 2.49 mm, etc.

Table 12 L. littoralis: First year mortality.

Length (mm)	Number of animals per Kg dry wt. fucoid	Mortality number	 flesh weight in g.	 shell weight in g.
1	714			
		359	0.0138	0.5987
2	355			
		267	0.0287	1.8686
3	88			
		65	0.0359	1.2085
4	23			
		9	0.0128	0.3009
5	14			
		6	0.0168	0.3650
6	8			
		0.3	0.0022	0.0500
7	7.7			
		-1.1	-0.0070	-0.1354
8	8.8			
		1.8	0.0196	0.2436
9	7.0			
		1.0	0.0165	0.3403
10	6.0			
		0.5	0.0127	0.2374
11	*5.5			
		Total	0.1530	5.0776
		Calorific value	0.7375 Kcals.	0.3184 Kcals.

* The 11 mm length group contains 11 animals. The growth rate of the juveniles (Fig. 11) indicates that the length group contains first and second year animals in equal proportion, i.e. 5.5 first year juveniles. The limits for the millimetre lengths are the same as for Table 11.

of approximately 11 mm (Fig. 14). The number of animals reaching the 11 mm group was 60.5 (i.e. 11 x 5.5). Shell growth ceases when the juveniles mature at the end of their second year. The adults live on average ten months (Guiterman 1970). Therefore the number of adults that were present represented 10/12ths of the animals surviving their second year. The mortality was therefore 24.7 (60.5 - 35.8). The average flesh and shell weight for this year group was 0.0589 g and 0.8863 g respectively. Thus the calorific value of the mortality was 8.38 Kcals.

The number of adults being eliminated annually was 35.8. The average flesh and shell weight of the adults was 0.0721 g and 1.2011 g respectively. Thus the calorific value of the mortality was 15.14 Kcals.

The total annual mortality was 35.38 Kcals (27.56 Kcals flesh and 7.82 Kcals shell).

The growth production (Pg) equals the mortality when the population is in a steady state condition, as was the littorinid population. Therefore the annual growth production of the littorinid population was 35.38 Kcals.

Discussion

The littorinids hatched at a shell length of 0.5 mm. The juveniles grew 10.45 mm on average in the first year and 4.11 mm in the second year (Table 10 and Fig. 14). Shell growth ceased at sexual maturity which was at the end of their second year. Guiterman (1970) measured the shell growth rate of a littorinid population in North Wales consisting of two juvenile size groups. The smaller size group's growth was about twice that of the larger group. The Derbyhaven first year juveniles grew 2½ times as much as the second year ones. Thus Guiterman's (1970) smaller and larger size groups would correspond to Derbyhaven's first and second year animals respectively. The Derbyhaven littorinids reached a size of approximately 10.95 mm by the end of their first year of growth and 15.06 mm approximately at sexual maturity. The shell growth rate increased from 0.26 mm/month in April and reached a peak in August of 1.75 mm/month before the rate decreased.

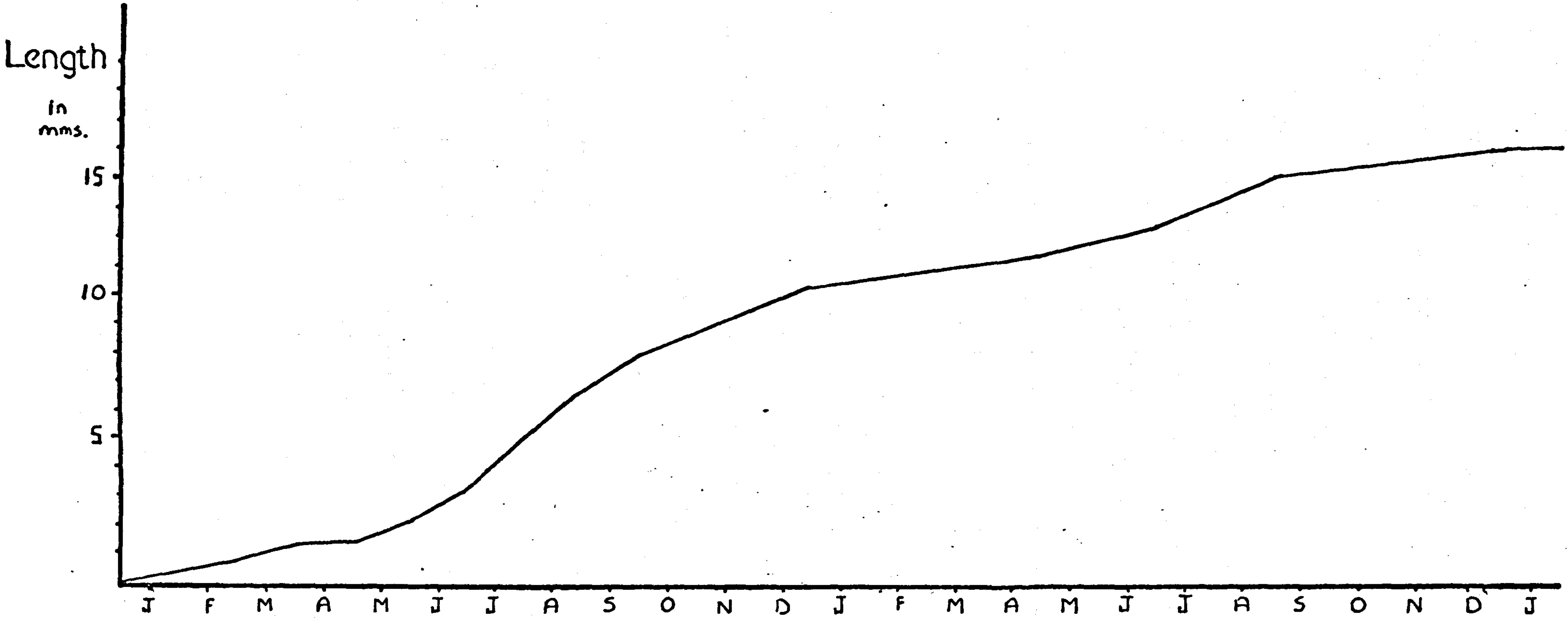


Fig. 14. The growth of a typical littorinid hatching at the beginning of January.

The changes in the shell growth rates correspond directly to changes in air and sea water temperature, an increase in the monthly temperature producing an increase in growth rate and vice versa. Guiterman (1970) also observed that the growth rate during the summer was greater than the winter, which suggests that the littorinids' growth rate is temperature dependent. The adult littorinids only live ten months on average (Guiterman 1970).

On the study ledge (Figs. 4 and 5) F. serratus and F. vesiculosus plants were intermixed and their biomasses were approximately equal. The littorinids were regularly transported, and therefore it was assumed that the littorinids found on the ten 100 g dry weight samples of F. serratus and F. vesiculosus collected each month when combined would represent the average population per kilogram dry weight fucoid. The length-frequency distribution of the littorinids collected from the samples did not significantly vary from month to month. However the length-frequency of the littorinids did vary between the fucoids (Table 11). F. vesiculosus supported $1\frac{1}{3}$ times as many adults and nearly double the number of newly hatched littorinids, while F. serratus supported more middle length animals (6 - 12 mm).

Barkmann (1955) observed a greater number of littorinids on F. vesiculosus compared to F. serratus. The larger number of newly hatched littorinids on F. vesiculosus corresponds to there being double the egg masses present on F. vesiculosus (Table 22). Many of the newly hatched littorinids were observed inside damaged vesicles of F. vesiculosus. F. serratus does not produce vesicles so F. vesiculosus will provide the littorinids with greater protection from water movements and probably predation. Experiments to study the relative attractiveness of the different species of algae indicate possible preferences by the littorinid, but results are contradictory. The attraction recorded by previous workers may be due to the stage of growth and freshness of the algae rather than to the species. In the laboratory the littorinids showed no preference between

F. vesiculosus and F. serratus. As the littorinids showed no apparent food preference between F. vesiculosus and F. serratus perhaps the protection for the newly hatched littorinids was the factor governing the greater number of adults on F. vesiculosus. The greater number of middle length animals on F. serratus may be due to the fact that it supports a lower density of mature and newly hatched littorinids.

The calorific content of L. littoralis was similar each month and the average value was 4.83 Kcals/g. The average calorific value of the littorinid population per Kg dry weight fucoid was 23.98 Kcals. The animal mortality and growth production was 35.38 Kcals of which the shell contributed 22%.

4. Nucella lapillus

Introduction

The dog-whelk is the only common carnivorous prosobranch on most rocky shores, occurring in large numbers within the balanoid zone. The upper limit of the species at most places is between E.H.W.N. and M.H.W.N. and the lower level lies between M.L.W.N. and M.L.W.S. On shores covered with barnacles the dog-whelk is most abundant at mid-shore levels (Southward 1953, Connell 1961).

Only Feare (1969) has undertaken a thorough investigation of the dynamics of dog-whelk populations. He observed that up to the third year of life it could be aged in the field using shell characters. Egg capsules were laid in March and August and hatched the following July and November (see reproductive chapter). This restricted breeding season led to the year groups being reasonably distinct until they matured. Moore (1938a) stated that growth stopped at maturity, and with a few exceptions this was true of this population, so that mature dog-whelks could not be aged. Up to maturity it was possible to ascribe individuals to an age group using the shape of the shell lip and the amount of shell weathering. (Weathering occurred during the winter, even though the animals were aggregated in clefts and pools at this time.) During the autumn, winter and spring the first year juveniles were distinguished from second year juveniles by size, while in the summer the presence of a weathered apex, with no weathering on the remainder of the shell, was diagnostic of first year juveniles. In second year juveniles most of the shell was weathered, but new growth appeared as a clean crescent behind the thin and sharp shell lip. When the juveniles matured the lip thickened and denticulate processes ('teeth') were laid down on its inner margin.

The age groups behave differently, dog-whelks in their first year migrating upshore and returning to lower levels in the second year. Adults lived and laid egg capsules on the low shore.

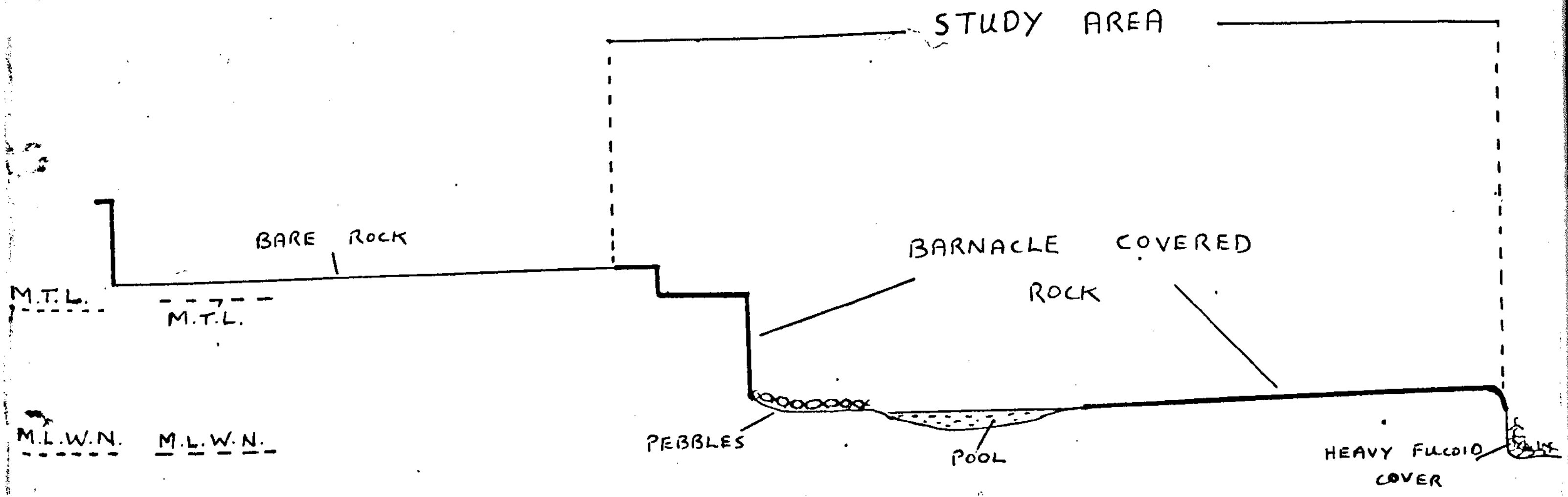
The shell length attained by the end of the first winter was related to winter temperatures, but the main growing season was from June to November. Adult size was attained in two years, after which the individuals did not usually grow, but those which did grow during the succeeding years may have been non-breeders or have been castrated by the trematode Parorchis acanthus.

Materials and method

The dispersion of dog-whelks on the shore was always non-random. During the summer all age groups formed aggregations (on barnacles) on the open shore. During the winter, adults and immatures aggregated densely in clefts and pools. This aggregation and migration behaviour posed serious sampling problems. However this was largely overcome by studying an area within which these migrations occurred (Figs. 5 and 15 and profile).

Fig. 15. The Nucella lapillus study area — showing the M.T.L. ledge face & the pebbles on the ledge below.

Profile of study area: --



The upper boundary was marked by an extensive area of bare rock on which very few dog-whelks were observed. The lower boundary was marked by the fucoid cover becoming very heavy and the barnacles disappearing. The lateral boundaries were less clearly defined. The study area of the M.L.W.N. ledge was raised, and on either side the fucoid cover was very thick and barnacles were absent. The M.T.L. ledge and the vertical face were defined by an inset on one side and an outcrop on the other.

Numerous dog-whelks (over 200) from within the study area were marked with waterproof paint and measured (from apex to siphonal canal) to the nearest 0.1 mm with vernier calipers every three or four weeks. These data enabled growth rates to be calculated.

The length of all the dog-whelks in the study area were measured each month.

Each month thirty dog-whelks were collected from outside the study area. The flesh was removed from the shell by dropping in boiling water for a few seconds and then gently breaking the shell. The flesh was dry weighed, part was used to determine ash content and part to determine calorific value using the Phillipson micro-bomb calorimeter. The shell length and weight of the animals were measured. Regressions of log shell weight and log flesh weight against log shell length were calculated. The lengths of all the dog-whelks of the monthly sample were substituted in the regression equations and their shell and flesh weights obtained. The calorific value of the flesh was derived using the conversion factor determined previously, and the shell calorific value using the same conversion factor (0.0627 Kcals/g) that was used for Patella vulgata.

Results

The young dog-whelks which hatched in July and August are referred to as the summer group and those hatching in November and December as the winter group.

There were few observations of animals under 6 mm, but those made suggested that growth was similar to those animals of between 6 and 17 mm (Table 13).

The newly hatched summer group dog-whelks grew rapidly in July and August (1.6 mm/month) before the shell growth rate decreased reaching a minimum in March (0.5 mm/month). The shell growth rate then increased reaching a peak in August (1.6 mm/month) and then decreased again reaching a minimum in March (0.13 mm/month). The shell growth rate then increased until the end of July when thickening of the shell took place. The shell growth decreased to cease by mid-October. The winter group dog-whelks showed a similar growth pattern and matured also in their third summer. Thus the shell growth for the winter group continued for six months longer than the summer group (i.e. 3 years compared to 2½ years). Therefore the average mature size of the summer group at 25.97 mm was nearly 2½ mm smaller than the winter group (28.32 mm).

The average shell growth (Fig. 16 and Table 13) for the first year was 12.17 mm, and during the second year the summer group grew 10.37 mm and the winter group 11.78 mm. The summer group juveniles' shell grew a further 3.43 mm and the winter groups' 4.37 mm in the third year before growth ceased at maturity.

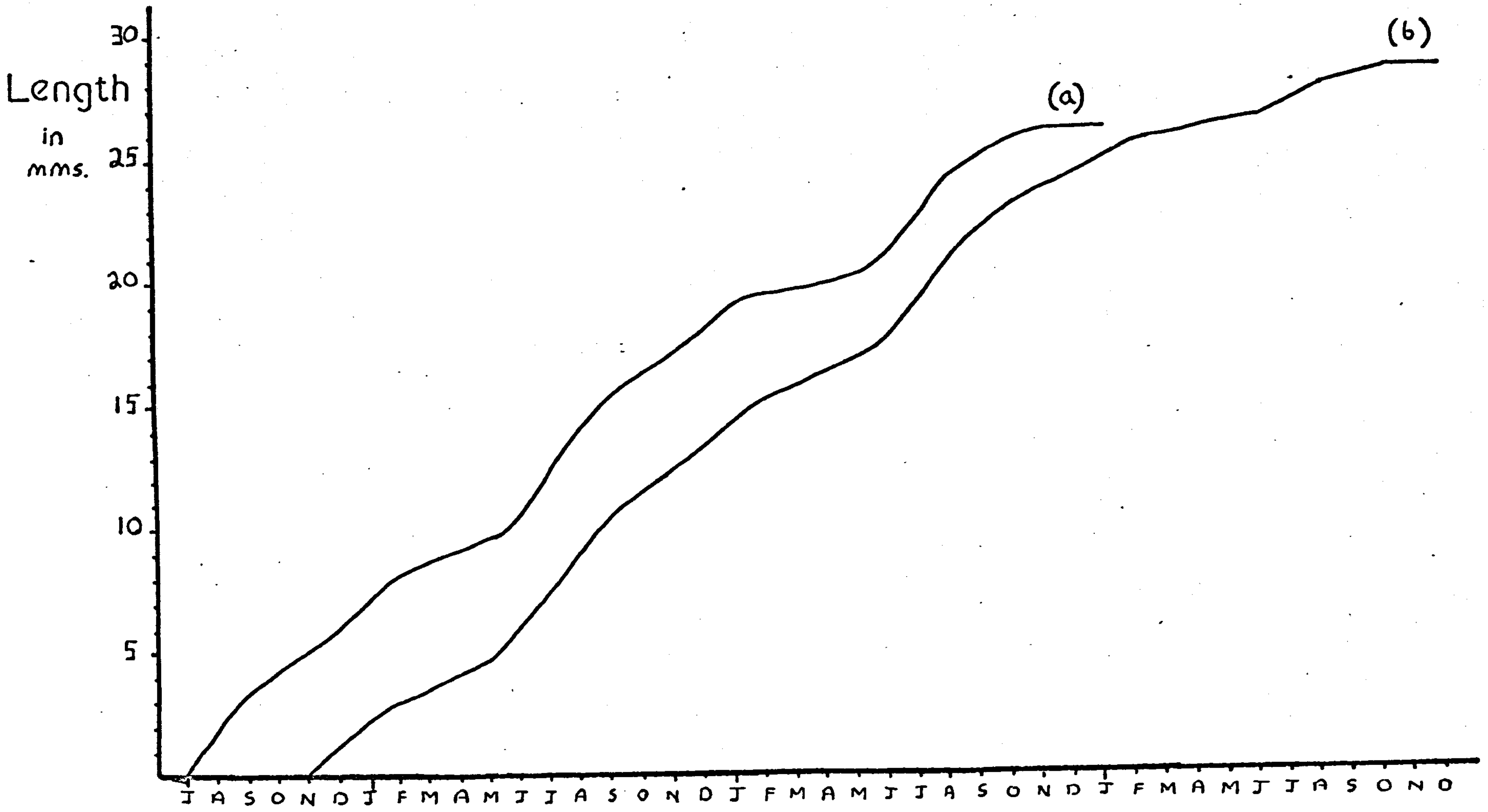


Fig. 16. Typical juvenile growth of N. lapillus hatching in the summer (a) and the winter (b).

Table 13 *Nucella lapillus*: The average monthly length and growth rate for the summer and winter group juveniles. - - - indicates shell thickening and —— that the animals have matured.

Month	Average length (mm)		Growth rate (mm/month)	
	summer	winter	summer	winter
July			1.56	
August	1.56		1.60	
September	3.16		0.82	
October	3.98		0.93	
November	4.91		0.95	0.95
December	5.86	0.95	1.09	1.09
January	6.94	2.04	0.95	0.95
February	7.90	2.99	0.50	0.50
March	8.40	3.49	0.50	0.50
April	8.90	3.99	0.64	0.64
May	9.54	4.63	1.13	1.13
June	10.67	5.76	1.50	1.50
July	12.17	7.26	1.56	1.56
August	13.73	8.82	1.60	1.60
September	15.33	10.42	0.82	0.82
October	16.15	11.24	0.93	0.93
November	17.08	12.17	0.95	0.95
January	19.12	14.21	0.19	0.95
February	19.37	15.16	0.28	0.50
March	19.59	15.66	0.13	0.50
April	19.72	16.16	0.44	0.63
May	20.16	16.79	0.88	0.83
June	21.04	17.62	1.50	1.30
July	22.54	18.92	1.56	1.57
August	¦24.11	20.49	¦0.70	1.68
September	¦24.81	22.17	¦0.67	0.85
October	¦25.48	23.02	¦0.49	0.93
November	|25.97	23.95		0.76
December	|25.97	24.71		0.72
January		25.43		0.19
February		25.62		0.28
March		25.90		0.18
April		26.08		0.22
May		26.30		0.44
June		26.74		¦0.75
July		¦27.49		¦0.38
August		¦27.87		¦0.45
September		|28.32		
October		|28.32		

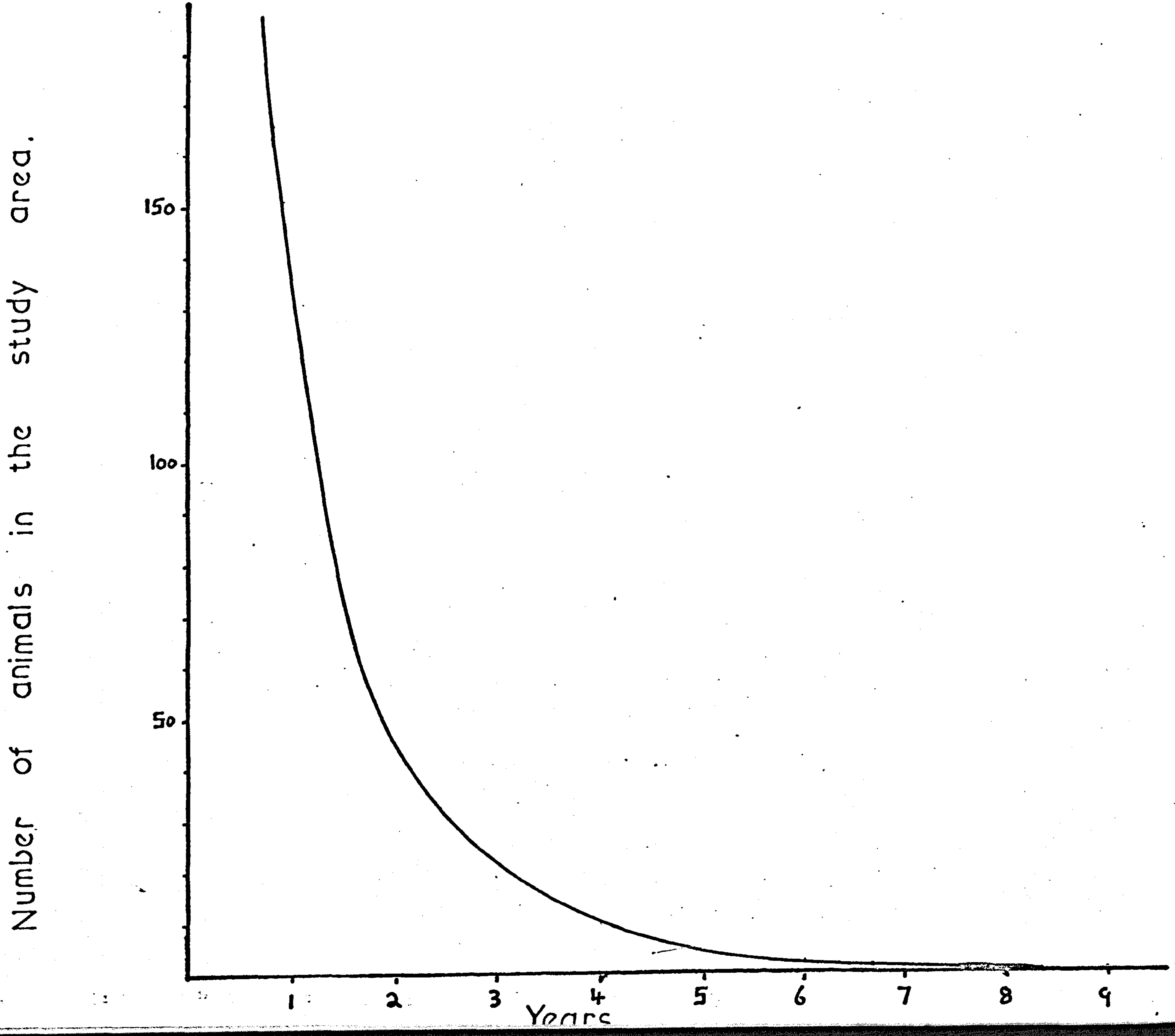
The correlation coefficient, intercept and slope of the adult and juvenile regression equations for flesh and shell weight are shown in Tables 14 and 15. The juvenile flesh weight per unit shell length increased from March to June and then remained constant until November when the weight decreased. The adult flesh weight per unit length increased from March until June and remained constant until November except for a decrease in weight during August. The weight then decreased from November reaching a minimum value in March. The juvenile shell weight per unit length remained constant. The mature animal's shell weight per unit length also remained constant but was heavier than a juvenile of the same length (e.g. a 25 mm juvenile shell weighed on average 2.1 g while a mature one weighed 2.5 g). When a juvenile animal matured the shell thickened and increased to the adult weight.

The calorific content of the flesh of the juveniles increased from March (4.76 Kcals/g) until June (5.22 Kcals/g) and then remained constant until November when the calorific value decreased. The calorific content of the adults' flesh increased from March (4.81 Kcals/g) until June (5.20 Kcals/g), then remained constant until November except for a decrease in August (5.02 Kcals/g). The rate decreased from November to March (Table 16).

The yearly mortality for the first, second, third year juveniles and adults was 90.2, 67.4, 58.7 and 45.5% respectively. The plot of survivors against age gave a life expectancy of 7 to 9 years (Fig. 17). During the study animals were observed to be at least 5 to 6 years old.

The calorific value of the flesh and shell for the juvenile and adult dog-whelks was determined each month. The length of all the dog-whelks in the study area were measured each month and their corresponding flesh and shell weights calculated from the regression equations. These weights were then converted to calories (Table 17 and Fig. 18). The area's adult flesh calorific value decreased from 54 Kcals in December to 32 Kcals in May, with

Fig. 17. A survival curve for the N.lapillus population.


Number of animals in the study area.
150
100
50
1
2
3
4
5
6
7
8
9
Years

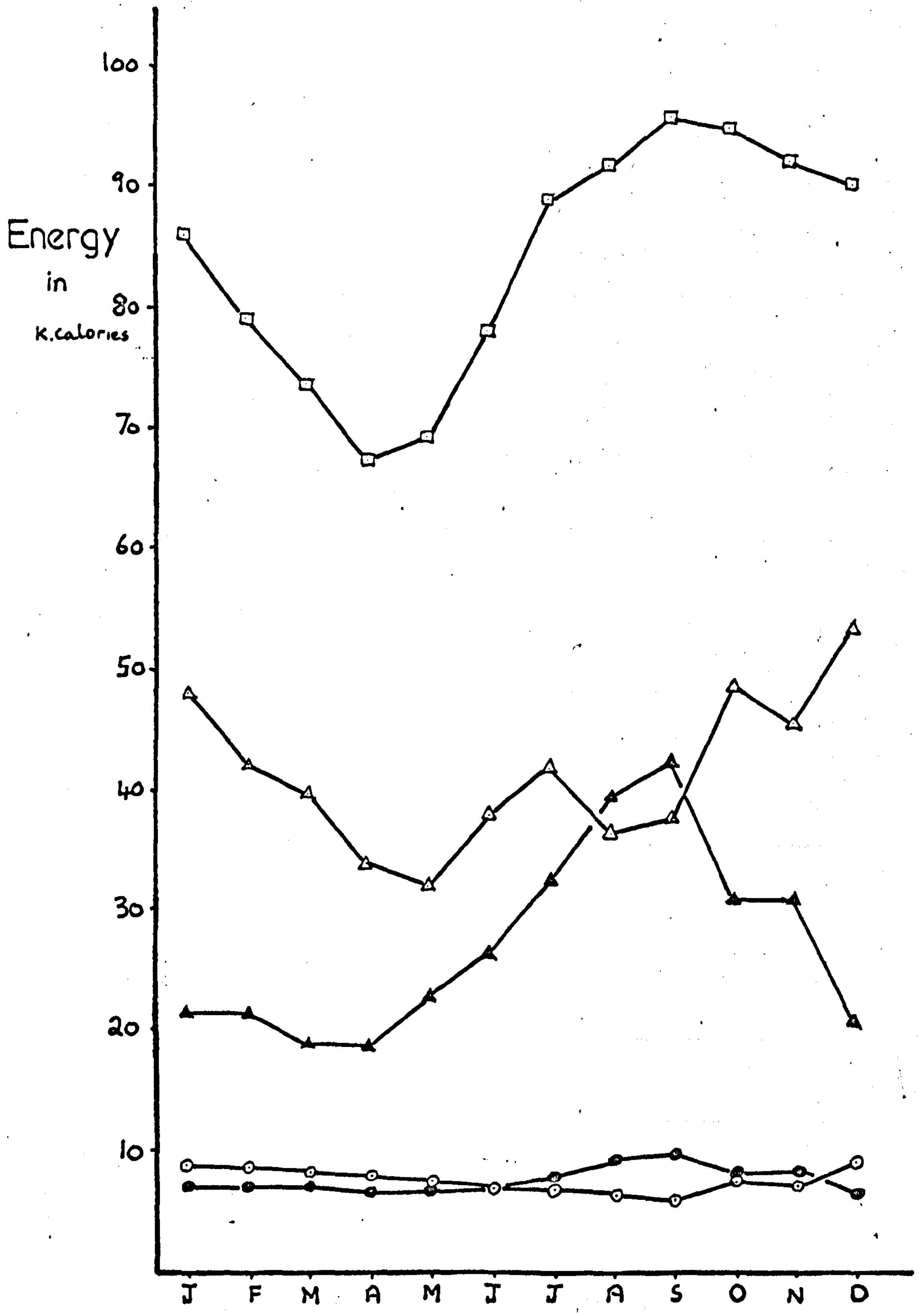


Fig. 18. The seasonal energy content of the N. lapillus population, biomass (□—□), adult flesh (△—△), & shell (○—○), juvenile flesh (▲—▲), & shell (●—●).

Table 14 *Nucella lapillus*: Parameters for the regression log flesh dry weight in g. against shell length in mm.

Month	Juvenile correlation coefficient	Juvenile intercept	Juvenile slope	Adult correlation coefficient	Adult intercept	Adult slope
January	93.46	-5.4196	3.1356	91.04	-3.5827	2.0055
February	96.89	-5.1879	2.9560	92.98	-3.8373	2.1686
				88.46	-4.1349	2.3611
March	96.66	-5.5981	3.2271	72.33	-4.3524	2.5030
April	98.43	-5.7957	3.3819	89.15	-4.9799	2.9173
May	96.53	-5.8104	3.4586	90.22	-5.0197	2.9438
June	96.25	-5.8409	3.4947	79.48	-3.8652	2.1865
				89.29	-3.1685	1.7442
July	98.23	-5.9887	3.6218	94.18	-3.4876	1.9451
August	96.84	-5.9973	3.6303	92.07	-3.3372	1.8500
September	96.46	-6.0106	3.6424	90.56	-3.2496	1.7949
October	95.85	-5.9620	3.5956	91.49	-3.1685	1.7442
November	96.31	-5.8539	3.4880	92.65	-3.1685	1.7442
December	94.69	-5.2890	3.0495	92.16	-3.3599	1.8643

Table 15 *Nucella lapillus*: Parameters for the regression log shell weight in g. agsinst shell length in mm.

		correlation coefficient	intercept	slope
Juveniles		99.22	-3.5510	2.7661
Maturing Juveniles	Aug. & Oct.	79.50	-3.1308	2.4752
	Sept. & Nov.	87.78	-1.6632	1.4743
	Oct. & Dec.	78.70	-1.5606	1.4143
Adults		89.72	-1.6363	1.4581

Table 16 *Nucella lapillus*: The calorific value of the juvenile and adult flesh each month.

Month	Juvenile				Adult			
	Kcals/g		Kcals/ash free g.		Kcals/g		Kcals/ash free g.	
January	4.76	±0.03	5.32	±0.04	4.90	±0.02	5.47	±0.02
February	4.75	±0.07	5.30	±0.08	4.81	±0.02	5.37	±0.02
March	4.76	±0.01	5.32	±0.01	4.81	±0.03	5.37	±0.04
April	4.77	±0.01	5.33	±0.01	4.83	±0.05	5.39	±0.05
May	4.99	±0.01	5.57	±0.01	4.97	±0.02	5.55	±0.02
June	5.22	±0.01	5.83	±0.01	5.20	±0.04	5.81	±0.05
July	5.22	±0.09	5.83	±0.01	5.20	±0.05	5.81	±0.06
August	5.32	±0.03	5.94	±0.03	5.02	±0.05	5.60	±0.06
September	5.24	±0.08	5.85	±0.09	5.19	±0.02	5.79	±0.03
October	5.24	±0.03	5.85	±0.04	5.21	±0.03	5.81	±0.03
November	5.10	±0.03	5.70	±0.03	5.19	±0.03	5.80	±0.03
December	4.93	±0.03	5.51	±0.03	4.99	±0.02	5.57	±0.03

Table 17 Nucella lapillus: Calorific values each month for the juveniles and adults of the study population.

Month	Juvenile flesh (Kcals)	Juvenile shell (Kcals)	Adult flesh (Kcals)	Adult shell (Kcals)	Total (Kcals)
January	21.58	7.10	48.15	8.98	85.81
February	21.48	7.10	42.41	8.46	79.44
March	18.99	6.99	39.53	8.29	73.80
April	19.02	6.81	33.93	7.93	67.69
May	22.94	6.72	32.21	7.58	69.45
June	26.71	7.11	38.07	7.05	78.95
July	32.37	8.04	41.85	6.70	88.96
August	39.48	9.33	36.59	6.53	91.94
September	42.53	9.87	37.72	6.17	96.29
October	31.00	7.99	48.57	7.73	95.30
November	30.95	8.62	45.01	7.19	92.27
December	21.07	6.44	53.54	9.34	90.39

a sharp decrease in March, and then gradually increased reaching a peak in mid-July of 42 Kcals. The calorific value decreased in August to 37 Kcals and in October to 45 Kcals, but increased in September to 49 Kcals and in November to 54 Kcals. The flesh calorific value of the juveniles decreased from December (21 Kcals) to April (19 Kcals) and then gradually increased reaching a peak in September (43 Kcals) followed by a decrease in October to 31 Kcals and in December to 21 Kcals. The calorific value of the adult shell for the area gradually decreased, except for increases in September and November. The calorific value of the juvenile shell for the area increased except in September and November when it decreased. The total dog-whelk biomass calorific value of the area increased from April (68 Kcals), reached a peak in September (96.29 Kcals) and then decreased.

As the dog-whelks in the study area were measured each month it was possible to calculate the monthly loss for each winter and summer year class. The annual mortality of juvenile and adult flesh and shell was the sum of their monthly loss. The annual juvenile mortality was 34.18 Kcals and the adult 28.88 Kcals, giving a total of 63.06 Kcals. (Table 18)

The growth production equals the mortality when the population is in a steady-state condition. The dog-whelk population was in a steady state. Thus the annual production was 63.06 Kcals (51.18 Kcals flesh and 11.88 Kcals shell).

Discussion

Moore (1938) observed that cessation of growth and an increase in lip thickness, frequently with deposition of teeth on the inner margin of the lip, accompanied the attainment of maturity. Feare (1969) stated that on some shores thickening of the lip and the secretion of teeth occurred regularly before maturity and that the processes were not, therefore, strictly related to maturity. Bryan (1969) showed the proximate factor inducing these changes was starvation, confirmed by Feare (1969). In the

Table 18 *Nucella lapillus*: The seasonal mortality of the juvenile and adult flesh and shell.

Month	Mortality (in Kcals)			
	Juvenile		Adult	
	flesh	shell	flesh	shell
January	2.04	0.68	2.18	0.40
February	1.72	0.58	0.74	0.17
March	1.44	0.57	1.55	0.36
April	1.80	0.67	1.55	0.36
May	1.71	0.52	2.28	0.52
June	2.23	0.62	1.94	0.36
July	2.51	0.67	1.03	0.17
August	3.79	0.73	2.01	0.36
September	3.16	0.62	3.20	0.71
October	2.85	0.54	3.44	0.55
November	2.30	0.60	2.23	0.36
December	1.43	0.40	2.05	0.36
Total	26.98	7.20	24.20	4.68

field starvation resulted from formation of non-feeding winter aggregations. Largen (1967) showed that feeding in dog-whelks stopped at low temperatures, and that activity was considerably reduced at temperatures below 5°C. Cowell and Crothers (1970) demonstrated that in juveniles tooth formation increased with exposure, and these individuals were more likely to be dislodged by the waves (and then swept away from their food supply) than those in shelter. In this study only the occasional (under 1%) adult was found with two or more rows of teeth. The juveniles on this shore therefore do not suffer starvation. This is because the mean monthly temperature remains well above 5°C and the shore is medium exposed with numerous crevices which the animals retreat into when the weather is rough to prevent dislodgement. Therefore on this shore lip thickening and teeth formation indicate maturation.

This thickening and teeth formation only took place in late summer and early winter in the juveniles' third year, thus the summer group mature at 2½ years and the winter group at 3 years. The winter group mature on average at a larger size (28.3 mm) compared to the summer group (25.97 mm), arising from the extra six months growth.

The juvenile shell growth rate was rapid in the first two years. The rate increased from April, reached a peak in August of 1.60 mm/month and then decreased reaching a minimum of 0.5 mm/month in March. The growth rate showed a direct correlation with temperature, an increase in the temperature producing an increase in the growth rate and vice versa. Feare (1969) also observed this correlation of growth with temperature. The shell growth rate in the juveniles' third year was slower and gradually decreased as thickening of the shell progressed and ceased when thickening was completed. When the animals matured there was no further shell growth (Table 13 and Fig. 15).

In the area the adult dog-whelk's shell calorific value decreased from January to September and increased in September and November. The decrease was due to mortality (3.79%/month) and the two increases corresponded with the two decreases in the area's juvenile shell calorific value in September and November. These two increases in the adult's shell calorific value corresponded to the third year winter and summer group animals maturing and entering the adult population. The area's juvenile shell calorific value remained constant from December to May and then increased reaching a peak in September. From December to May the shell growth rate was low and mortality equalled the growth; however during the summer the shell growth rate was higher and there was an increase in the area's juvenile shell calorific value as the growth was greater than the mortality. The two decreases in September and November correspond to the third year juveniles maturing and leaving the juvenile population (Fig. 18).

The adult's flesh calorific content decreased from December to April (4.83 Kcals/g) and then increased reaching a peak in June (5.20 Kcals/g). The calorific content then remained constant until December except for a decrease in August (5.02 Kcals/g) (Table 16). The winter decrease coincided with the adults aggregating in crevices and pools. The adults were not observed to feed during this period (Table 50). Moore (1938b) showed that the tissue weight of mature dog-whelks dropped sharply in February and March and then began to increase. He observed no such drop in immature animals. Moore (1938b) ascribed the weight decrease either to a loss in reproduction products or cessation of feeding by the mature dog-whelks during the main spawning period from February to March. The decrease in calorific content of the adult's flesh at Derbyhaven was probably due to the depletion of storage tissues as the adults did not feed during this period. The main storage component of <u>N. lapillus</u> is lipid which has a calorific content of 9.45 Kcals/g. The calorific content of proteins and carbohydrates is much lower, 5.65 and 4.10 Kcals/g respectively. Thus any increase or decrease of its lipid stores will affect the calorific content of the animal. However it was noticed that a comparatively greater decrease in calorific content occurred in March.– The adults spawn during March so the calorific loss during this month will have been due to the loss of reproductive products as well as a further depletion of the storage tissue. The adults began feeding again in May and the calorific content increased. This increase will have been due to the storage tissues being replenished. There was a slight decrease in the calorific content of the flesh in August. The adults aggregate and breed during August, so this loss in calorific content will have been due mainly to the loss of reproductive products and also due to a depletion of the storage tissues.

The calorific content of the juveniles' flesh increased in April (4.77 Kcals/g), reached a peak in June (5.22 Kcals/g) and remained constant until November when it decreased until January (Table 16). This decrease coincided with the juveniles aggregating. However unlike the adults the juveniles feed during the winter and were observed feeding on days when the sea was calm. The time of feeding was greatly reduced compared to the summer (Table 50), and was probably not enough to maintain the animal so the decrease in calorific content in the winter will have been due to the depletion of the storage tissues.

The mortality was very high in the first year, 94.5%. The second and third year juvenile mortalities were 67.4% and 58.7% respectively. The annual adult mortality was 45.5% on average and longevity was estimated as up to nine years (Fig. 17). Feare (1969) estimated a similar high first year mortality ($\simeq$ 90%), second year as 52.2% and third year (adults) as 27.1%. Feare calculated the expectation of mature life using the formula $Ex = \frac{2-m}{2m}$ (Lack 1954) as 3.2 years, giving a longevity of 5 to 6 years. The adult longevity in this study calculated by the formula was 1.7 years, giving a longevity of 5 years. Mature animals marked in the summer 1973 were recovered in the winter 1976, when they must have been in at least their sixth year. Moore (1938a) stated that dog-whelks survived up to 7 or more years. The annual juvenile mortality was 34.18 Kcals and the adults

28.88 Kcals, giving a total of 63.06 Kcals for the study area (Table 18).

The annual growth production of the study area was 63.06 Kcals.

CHAPTER 3

REPRODUCTIVE PRODUCTION

1. General Introduction

This chapter discusses the estimation of the energy content of the gametes liberated during spawning (Pr in the energy equation) over the course of the year.

It was possible to dissect out and weigh the gonads of the limpet and dog-whelk and calculate a relationship between shell length and gonad weight. Animals were collected each month and a regression of log weight on log length calculated. The change in gonad weight at spawning enabled the gamete production to be calculated.

Unfortunately it was found impossible to dissect out the gonads of the littorinid as the gonads ramify intricately through the visceral mass. However it was possible to collect the egg masses deposited on the fucoids. Therefore each month the egg masses were removed from a known weight of fucoid and weighed. The number and calorific value of adult littorinids per weight of fucoid was known (see growth production chapter) so the production of egg masses per adult could be calculated. It was assumed that the egg masses represented the total gamete production.

2. Patella vulgata

Introduction

Extensive data are available on the reproductive cycle of this species. Orton and his co-workers (Orton 1920, 1928, Orton et al. 1956) carried out detailed studies which have since been verified and extended (Das and Seshappa 1948, Ballantine 1961, Blackmore 1969, Lewis and Bowman 1975). P. vulgata is a consecutive hermaphrodite which spawns once a year in late autumn or early winter. Orton et al. (1956) found that the time involved in maturation and spawning depended upon the locality, more northerly populations taking longer to complete the cycle than those in the south.

Since P. vulgata possesses no known secondary sexual characters, sexing is based on the gonads which are in a resting condition with small gonads for much of the year, so that the sexes are indistinguishable. Fortunately the sex can be distinguished by colour once the gonads commence developing, as fully described by Orton et al. (1956). The male gonad is pinkish white or cream, and the female green or brown. Orton distinguished five stages of gonad development, based on the size of the gonad relative to the whole visceral mass (Table 19). Ballantine (1961) criticised the way in which the index was actually used by Orton. In the first place it is mathematically improper (and biologically misleading) to treat the stages as if they were additive, which is what Orton did in calculating the 'mean state of development' of each sample. The volume of the gonad in stage V is clearly more than five times that of stage I. So Ballantine produced a conversion of the index expressing each stage as a relative volume of the visceral mass (Table 21). Thus using the conversion the different stages can be added and a proper average given for the sample. A second criticism is that Orton did not take adequate steps to investigate or allow for possible variation in relative gonad size with age. Ballantine found that the testes of third year males were relatively smaller at all stages of development (just under half the relative size at spawning) than the older male limpets. Also Ballantine found that the ovaries were consistently smaller than the testes during the breeding season.

Orton's gonad index indicates the timing and pattern of the gonad cycle, which though improved by the use of Ballantine's conversion does not give a quantitative picture of the gamete production. The problems are that the gonad index assessment is entirely subjective and has only five stages to describe what must be a continuous process. Also the index measures only relative volumes of the gonads, not the absolute ones, and it is quite possible for the volume of the visceral mass to alter. Such alterations would affect the interpretation of the results but would not be detectable or measurable. Finally the density of the gonad could vary

Table 19 *Patella vulgata*: The average stage of gonad development for the third year males, fourth year and older males and females. The development was expressed as an Orton Index stage and as the gonad weight / flesh weight.

Month	Orton Index Stage			$\frac{\text{Gonad weight x 100}}{\text{Flesh weight}}$		
	Males			Males		
	Third year	Fourth & older	Females	Third year	Fourth	Females
1974						
March	0	0	0	3.1	3.3	3.3
April	0	0	0	3.1	3.3	3.3
May	0	0	0	3.1	3.3	3.3
June	0	0	0	3.1	3.3	3.3
July	0	I	I	3.1	4.5	4.0
August	II	III → IV	III	5.1	16.3	11.7
September	III	IV → V	IV	9.5	26.2	22.6
October	III → IV	V	V	14.0	34.2	31.2
November	V	V	V	15.1	31.4	28.7
December	IV → III	III → II	III → II	14.6	17.8	17.8
1975						
January	I	II	I	5.0	11.2	5.6
February	0	I	0	3.1	6.0	3.3
March	0	0	0	3.1	3.3	3.3
April	0	0	0	3.1	3.3	3.3
May	0	0	0	3.1	3.3	3.3
June	0	0	0	3.1	3.3	3.3
July	0	0 → I	0 → I	3.1	4.5	4.0
August	0	III → IV	III → IV	3.1	11.1	10.6
September	II → III	III → IV	III → IV	6.0	15.5	14.9
October	III	IV	IV	8.3	19.0	18.6
November	III → IV	IV → V	IV	11.4	27.1	26.8
December 4th	IV	IV → V	IV → V	15.2	32.7	31.1
December 20th	V	V	V	19.4	40.6	37.1
1976						
January	III	III	III	12.2	21.3	18.2
February	I	II	I	9.8	9.8	6.0
March	0	I	0	5.0	5.0	3.3

Table 20 *Patella vulgata*: Calorific values of male and female gonads.

	Month	Stage	Kcals/g	Percentage ash	Kcals/ash free g.
Male		developing			
	August (1975)	II — III	4.69 ±0.04	10.90	5.26 ± 0.04
	September (1975	III — IV	4.71 ±0.17	10.89	5.29 ±0.19
	November (1974)	V	4.73 ±0.11	10.39	5.28 ± 0.13
	October (1974)	V	4.73 ±0.11	10.41	5.28 ± 0.12
	December (1975)	V	4.73 ±0.11	10.44	5.28 ± 0.12
		spent			
	December (1974)	III — II	4.58 ±0.10	11.97	5.20 ±0.11
	January (1975)	II — I	4.55 ±0.05	12.03	5.17 ±0.05
Female		developing			
	August (1974)	II	4.74 ±0.03	10.53	5.30 ± 0.03
	September (1975)	III — IV	5.97 ±0.07	9.77	6.61 ±0.07
	September (1974)	IV	5.98 ±0.09	9.45	6.60 ±0.10
	October (1974)	V	6.04 ±0.07	9.36	6.66 ±0.08
	November (1974)	V	6.04 ±0.09	9.21	6.65 ±0.10
	December (1975)	V	6.01 ±0.19	9.35	6.63 ±0.21
		spent			
	January (1976)	IV — III	5.41 ±0.12	11.27	6.10 ±0.13
	January	II — I	4.52 ±0.07	12.93	5.19 ±0.08

Table 21 A comparison of Orton's gonad index, Ballantine's conversion of Orton's index and from this study the weight of the gonad expressed as a percentage of flesh weight (somatic tissue plus gonad) for each of Orton's index stages. The somatic tissue weight used was that of an animal the same length in June (see method section).

Orton's gonad index		Ballantine's conversion	Gonad weight/flesh weight x 100		
Stage			Third year males	Fourth year & other males	Females
0:	Inactive or neuter		3.1	3.3	3.3
I:	Beginning to develop, sex detectable but only a slight increase in size	2.75	3.5	4.5	4.5
II:	Developing to $\frac{1}{3}$ full size	8.0	5.7	7.7	7.7
III:	Between $\frac{1}{3}$ and $\frac{2}{3}$ full size	20.0	8.0	12.5	12.5
IV:	$\frac{2}{3}$ full size	47.0	11.0	18.8	18.8
V:	Fully developed	63.0	12.8	26.7	24.4

without detection, and thus there is no direct connection between the number of gametes produced and the gonad index.

Material and method

At the beginning of each month sufficient animals were collected to determine the sex ratio and the stage of gonad development for each year group and sex. The animals were collected on the study ledge away from the quadrats (Fig. 5). The flesh was removed whole from the shell by dropping into boiling water for a few seconds. In both sexes the gonad forms a discrete solid body situated on the ventral side of the visceral mass adjacent to the foot. The gonad was easily revealed by cutting peripherally through the visceral membrane and deflecting the visceral forwards from the foot. The gonad was expressed as a percentage volume of the total flesh and a monthly average given for each year group and sex. As the gonads were inactive for much of the year over 1,000 animals were sexed over the period, September to November, when the gonads were well developed, so as to determine the sex ratio for each year group.

Each month the dry weight of gonad and flesh of thirty animals was measured. The dry weight of the gonad was expressed as a percentage of the dry weight of the flesh, i.e. gonad plus somatic tissue, and also as a percentage of the flesh weight but using the somatic tissue weight of an animal the same length in June (the somatic weight was determined from the regression of log somatic tissue weight against log shell length for June, Table 21). The two average percentages were calculated each month for both sexes and each year class.

The gonad dry weights were converted to calories using the calorific values determined each month from the dry weight samples of the gonad tissue using the Phillipson micro-bomb calorimeter.

Results

All the first and second year limpets were neuter. All third year, 92.5% of the fourth and 58% of the limpets older than four years, were males. Thus 7.5% of the fourth year and 42% of the limpets older than four years were females.

Each month the average stage of gonad development for both sexes and each year class was expressed as a percentage of the total flesh volume. Also each month the weight of the gonad and flesh for the average stage of development was determined. The average gonad condition was then expressed as a percentage of the flesh weight (Table 19). In females the rate of gonad development and the percentage gonad weight at each developmental stage were similar for each year class. This was not so for the males, where in the third year the gonads developed later in the year, and the percentage gonad weight was consistently lower than in fourth year and older males.

Each month the total gonad weight was calculated for the quadrats' population of third year males, older males and females. This was possible using the average gonad weight as a percentage of the flesh weight for each sex and age class (Table 19), the regression of flesh weight on shell length (Table 4) and the length of each limpet within the quadrats (see previous chapter).

These gonad weights were converted to calories (Table 20). The calorific value of the gonads of the quadrats' limpet population for each month are shown in Table 7.

The gonad weight at each stage of development for both sexes and year groups was expressed as a percentage of the flesh weight. The somatic flesh weight used in this calculation was that of an animal of the same length in June. The somatic flesh weight in June was used as during this month the somatic tissue was at its full size and weight. When the gonads commenced development in August the somatic tissue size and weight decreased. Thus by using the somatic tissue weight of an animal the same length in June (determined from the regression equations, Table 4) the real change in gonad weight for each of the stages was measured (Table 21).

At each stage of Orton's index the gonad weight as a percentage of flesh weight had the same value for both fourth year and older males (Table 21). The percentage weight of the inactive gonad was 3.3%, and when fully developed in stage V was 26.7%. The values of the other stages were in between these two. The females had a similar percentage gonad weight at all stages except stage V when they were fully ripe at 24.4% compared to 26.7% for males. The third year males had a lower percentage gonad weight for each of Orton's index stage, reaching a maximum value of only 12.8%.

The gonads of the fourth year and older males started developing at the beginning of July in 1974 (Table 19). The development was rapid and stage V was reached by November. Spawning commenced at the beginning of December. The gonads had reverted to their inactive state by mid-February and remained inactive until July. The gonads then developed quickly reaching a stage in between III and IV. Development was then much slower until December when the gonads quickly matured and spawning commenced almost immediately after maturation. The gonads had reverted to the inactive stage by March. In 1974 the third year males' gonads commenced development at the end of July and slowly reached maturity by November and spawned soon after maturation. The gonads had reverted to the inactive stage by mid-January. In 1975 the gonads did not commence development until September. The gonads matured in mid-December and spawned immediately. The gonads had reverted to an inactive stage by mid-February.

The female gonad development was similar to that of fourth year and older males except that development commenced five to fifteen days later than in the males. The females matured and spawned at the same time as the males. The female gonads reverted to an inactive stage about two weeks before the males.

The calorific content of the gonads increased with development.

The male calorific content increased from 4.69 Kcals/g at index stage II to III reaching 4.73 Kcals/g at stage V. The calorific content decreased as the gonad became spent, reaching 4.55 Kcals/g at stage II to I. The female gonad calorific content increased from 4.73 Kcals/g at stage II reaching 6.04 Kcals/g at stage V. The calorific content decreased as the gonad became spent, reaching 4.52 Kcals/g at stage II to I (Table 20).

The gamete production was estimated as the difference between the calorific value of the gonads when ripe (stage V) and the inactive stage. This was calculated for 1974 in mid-November, and for 1975 at the end of December when all the breeding limpets were ripe (Table 7). The gametes lost to the quadrats population due to mortality when the gonads were developing were also added to give the total gamete production. The gamete production for 1974 and 1975 was 113.6 Kcals and 114.5 Kcals respectively.

Discussion

P. vulgata was neuter until its third summer when the majority matured and became male. In their fourth year a small percentage (7.5%) underwent a sex change and became female; this increased to 42% in their fifth year. This sex change takes place during the gonadal resting stage and therefore cannot be observed macroscopically. There was no evidence to suggest a greater growth rate or mortality in females, so one can assume that the sex change occurs only during the fourth and fifth years of their lives and that just over 50% remain male. This sex change phenomenon in limpets is well known. Das and Seshappa (1948) and Lewis and Bowman (1975) observed a 50/50 sex ratio among the older animals, while Ballantine (1961) found the ratio varied for 50 to 80% females. These authors observed the sex change to occur between the limpets' third and sixth year, which is similar to this study. While Orton et al. (1956) and Blackmore (1969) recorded that the female proportion continually increases though at a diminishing rate with size, males were always found even in the oldest age group. The present observations and those of the other authors may suggest that P. vulgata is diandric, i.e. that there are two genetically different males, one that will undergo a sex change and one that does not.

Orton's index indicates the timing and pattern of the gonad cycle. However certain inherent disadvantages prevent it from giving a completely quantitative picture of the gamete production as stated in the introduction. These problems were overcome in this study by weighing the gonads. The gonad weight was expressed in two ways. The gonad weight each month was expressed as a percentage of the flesh weight. This enabled the gonad weight of the quadrats' population to be calculated using the regression of log flesh dry weight on log length. The gonad weight / flesh weight percentage for each of the index stages varied tremendously, e.g. stage V in November 1974 of a fourth year or older male, the gonad percentage was 31.4%, while in December 1975 was 40.6% (Table 19), as the calculated percentage depended not only on the gonad weight but the somatic tissue weight as well. Thus any change in the somatic tissue weight will alter the percentage without there being any change in the gonad weight. The gonad weight at each stage of development was expressed as a percentage of the flesh, but the somatic tissue weight used in the calculation was that of an animal the same shell length in June. Thus any change in the percentage will be due to a change in the gonad weight. June was chosen as the somatic tissue was at full size and weight and was the month prior to the commencement of gonad development. As a change in the percentage was due only to a change in the gonad weight the index stage can be directly compared (Table 21). Ballantine's (1961) conversion figures for Orton's index stages differ from this study. Ballantine calculated the gonad volume as a percentage of the visceral mass i.e. somatic tissue, while in this study the gonad weight was calculated as a percentage of the flesh (somatic plus gonads).

The females, fourth year and older males all maintained the same relative gonad size up to stage V of the development cycle (Table 21). The males were observed to commence gonad development one or two weeks before the females. The rate of development was similar for females, thus as both sexes ripen around the same time the male gonads were larger when ripe, 26.7% compared to the females 24.4%. Ballantine (1961) found that the female gonads at spawning were between 3/5ths and 4/5ths the size of the male gonads. The difference found at Derbyhaven was not as great, and also Ballantine does not mention any time difference in the commencement of gonad development. The gonads of the third year males at all stages of the cycle were relatively much lighter than those of the corresponding older males and females. These third year males reached a maximum value when ripe of only 12.8% i.e. under half of the corresponding value for older males. Ballantine also found that the third year male gonads at spawning were just under half the size of the older males.

Using the percentages calculated in Table 21 for Orton's index stages a figure was constructed showing the seasonal changes in the gonad weight for the third year males, fourth year and older males and females (Fig. 19).

The females, fourth year and older males commenced gonad development during July in 1974. The males began development a week or two before the females. The animals were fully mature by October though spawning did not take place until mid-November. Spawning was sudden and appeared to be synchronous for the population. Approximately 60% of the gametes were released in the first two weeks and over 90% by mid-January. The gonads did not return to their resting stage weight until the end of February. The males released their gametes at a slightly slower rate than the females. In 1975 the gonad development commenced as in 1974, during mid-July. The development up to early September, to a stage between III and IV, was similar to that in 1974, but after this the development was much slower. The gonads in 1975 did not ripen until mid-December, nearly two months later than in 1974. However spawning commenced more or less immediately after ripening, unlike 1974 when there was a month between the two events. Gamete release was rapid and followed a similar pattern to that of 1974. The third year

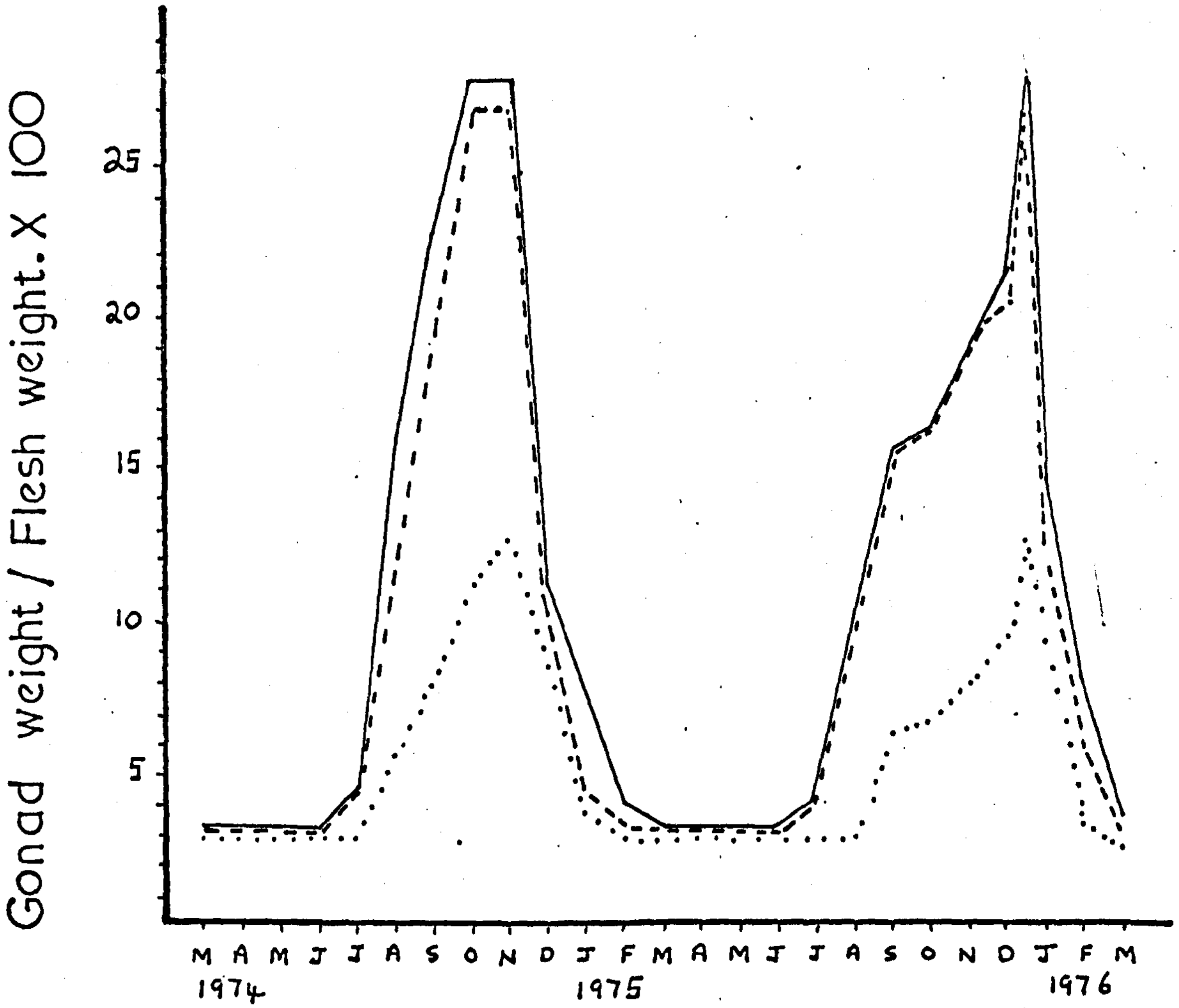


Fig. 19. *Patella vulgata*: The seasonal change in the gonad weight, expressed as a percentage of the flesh weight. Fourth year & older males (——), third year males (……) and females (- - -).

males' gonads began developing a month later than the older animals in 1974. Also the development was slower but spawning was synchronous with the rest of the mature animals. Similarly development in 1975 commenced over a month later than the older animals, but otherwise followed the same pattern as the adults.

Ballantine (1961) observed that individuals spawned up to 90% of their gametes in a short period of time and that the remainder of the gametes were visibly deformed, broken or unripe, suggesting that all the ripe eggs had been spawned. The number of eggs then decreased slowly with a rapid increase in the proportion of broken and deformed eggs, suggesting that resorption was taking place. This would support the observed phenomenon i.e. the sudden and rapid decrease in gonad weight, up to 90% in the first five to six weeks while another six to eight weeks are required for the gonads to revert back to their resting stage weight.

So far the average gonad development has been discussed. Though spawning appeared to be synchronous for the population, some animals must either spawn much more slowly or in several phases, as animals were found still at a post-spawning stage IV to III in January 1974 and a few at stage II any time between February and July when the rest were in the inactive stage. Lewis and Bowman (1975) observed that at stage V by reference to size, colour and external morphology the gonad may still possess some developing stages. This study found a few gonads at stage II between February and July, so some limpets may have ripe gametes between February and July. Artificial fertilisation has been effected in April and recorded as late as June by Dodd (1957). Therefore spawning could extend over six months, but whether or not spawning and fertilisation does occur naturally in the spring and summer and the contribution, if any, they would make to the total reproductive capacity, is unknown. Nevertheless there is some potential for an extended settlement period which might account in part for the progressive increase in juvenile numbers that characterized the recruitment pattern and for the small size of some juveniles at the end of their presumed first year of shore life (Figs. 6, 7 & 8). Choquet (1968), while showing that gonad activity was most intense from July to December, clearly favours a very extended breeding period since he recognized distinct groups of juveniles settling in all four seasons of the year.

P. vulgata was observed to spawn at the end of November in 1974 and December in 1975, showing clearly a considerable annual variation in the period of development and onset of spawning. The development of the gonad differed in the two years. In 1974 the development was more rapid and spawning was earlier than in 1975. It was observed that the monthly average temperature in the autumn of 1975 was significantly higher than in 1974. Possibly initiation of the development cycle depends on the time of year, and the later stages on the temperature. In 1974 the average temperature around the few days that spawning commenced was 9.9°C and in 1975 was 9.8°C. Orton et al. (1956) suggested that heavy onshore winds and waves were the trigger for the start of spawning. These conditions were present when spawning took place, though in both years these conditions were present during most weeks of the autumn. Lubet (1955) showed that in Mytilus edulis spawning was not possible before the release of neurosecretory granules from the visceral and cerebral ganglia, but when this had occurred a sharp change in temperature or mechanical stimulation could trigger off spawning. In many marine organisms with external fertilisation gametes (or gamete extracts) can stimulate spawning. A severe gale is likely to be accompanied by sharp changes in air (and possibly inshore sea) temperatures. The generated waves will produce increased mechanical stimulation of all kinds. The gametes of some limpets will probably be forcibly released if the gonad is sufficiently developed. Thus three possible spawning stimuli will be present at the same time, and most probably all three reinforce one another to ensure the rapid synchronous spawning.

As can be expected for a steady state population the gamete productions for 1974 and 1975 were very similar. The gamete production in 1974 was 113.6 Kcals and in 1975 114.5 Kcals. However this may be an overestimate of the gametes spawned as possibly up to 10% of the gametes were resorbed.

3. Littorina littoralis

Introduction

The adults and juveniles have a similar distribution, probably due to the lack of a planktonic stage. The male littorinid does not release its gametes directly into the environment, but transmits sperm to the bursa copulatrix of the female during copulation. Fretter and Graham (1962) and Linke(1933) reported that both the sperm and carrier nurse cells enter the seminal receptacle, and those still attached to one another are stored, while free sperm and nurse cells are ingested, and digested. A considerable amount of male gamete production, therefore, is diverted into providing nourishment for the female, and released eventually to the environment in the form of female tissue, metabolites, and other organic compounds. The male and female gamete production are probably very similar. Spawning usually takes place at night, a few hours after copulation, and the gelatinous egg mass is deposited on damp fucoid fronds. Spawning never takes place on other algae. The spawn is flat and may be kidney-shaped in outline, measuring 7 x 3 mm (Linke 1933, Lebour 1937), oval or circular. Fretter and Graham (1962) state that the egg masses consist of 90 - 150 eggs, while Guiterman (1970) states 112 to 270. Thorsen (1946) states that the incubation time for the eggs is 3 to 4 weeks at 13 - 14°C. Guiterman (1970) observed that the incubation time depended on the season, in winter 9, spring 7, summer and autumn 3 weeks.

Sexual maturity of the female is judged by the condition of the oviduct, capsule and accessary gland. The females are mature if the oviduct is full of reproductive material and the glands are swollen. Guiterman (1970) established that animals without swollen oviducts and glands were not mature. Guiterman(1970) observed that throughout the year all females which were not parasitised and which were fully grown were found to possess swollen oviducts and glands. As at all times of the year egg masses were found on the shore, females once mature probably continue to lay eggs until they die or become infected with parasites. The males can easily be identified by the large penis. The gonads of both sexes are diffuse and extremely difficult to dissect out. Guiterman (1970) measured fecundity by collecting the egg masses.

Materials and method

The egg masses were removed from the fucoid samples taken each month (see page 31). The egg masses were converted to calories using the calorific values determined from dry weight samples of the egg masses, using the Phillipson micro-bomb calorimeter. The spawn deposited each month was calculated by taking into account the incubation times observed by Guiterman (1970) i.e. winter 9, spring 7, summer and autumn 3 weeks.

The adult littorinids obtained from the samples collected each month were sexed and the sex ratio determined.

Results

The sex ratio was unity. The calorific value of the newly deposited spawn was 5.41 ± 0.2 Kcals/g or 6.04 ± 0.22 Kcals/ash free g, with an ash content of 10.45% . The sperm deposited annually per kilogram dry weight of <u>F. serratus</u> and <u>F. vesiculosus</u> was 13.68 and 26.12 Kcals respectively, giving an average of 19.91 Kcals/dry Kg fucoid (Table 22). The average spawn production per female, living 10 months, was 1.11 Kcals.

Discussion

The calculated spawn production each month varied but no seasonal pattern was apparent (Table 22). Approximately double the spawn was deposited on <u>F. vesiculosus</u> compared to <u>F. serratus</u>. This was partly explained by <u>F. vesiculosus</u> supporting approximately 1$\frac{1}{3}$ times the number of mature animals. However the spawn deposited per adult was 0.76 Kcals compared to 0.55 Kcals. This difference would imply that the littorinids show a definite preference to spawn when on <u>F. vesiculosus</u>.

The male does not release its gametes directly into the environment

Table 22 *Littorina littoralis*: The dry weight of the egg masses deposited each month per kilogram dry weight of *Fucus vesiculosus* and *F. serratus*.

Month	Egg mass weight (g. dry wt.)	
	F. vesiculosus	F. serratus
January	0.16	0.22
February	0.07	0.06
March	0.33	0.04
April	0.51	0.30
May	0.03	0.39
June	0.40	0.21
July	1.36	0.13
August	0.06	0.52
September	0.25	0.13
October	0.53	0.10
November	0.84	0.35
December	0.29	0.08
Total (g)	4.83	2.53
Calorific value (Kcals)	26.13	13.68

but transmits them to the female. Thus the annual reproductive production (Pr) released into the environment is just the spawn deposited by the females. The annual spawn production was 19.91 Kcals/Kg dry weight fucoid. The average spawn production per female, living 10 months, was 1.11 Kcals which was very similar to that observed by Guiterman (1970). Guiterman determined that an average female in its lifetime laid 8,040 eggs with an approximate calorific value of 1.2 Kcals.

4. Nucella lapillus

Introduction

Dog-whelks are gonochoristic, and fertilisation is internal (Fretter, 1953). The sex can be determined by the presence or absence of a penis. In both sexes the gonad lies dorsal to the digestive gland (Fretter and Graham 1962) with which it is intimately associated. The external appearance of both male and female gonads varies during the reproductive cycle, and in addition the capsule gland of females, situated anterior to the ovary, displays an annual cycle of size and colour change. The gonads of unripe males are small and green or greenish-yellow, but as spermatogenesis proceeds they gradually become predominantly red or yellowish-orange. The colour change becomes more rapid, passing through orange to brick-red or reddish brown and the colour may spread to the head and foot. White areas of ripe sperm appear on the columellar side of the whorl. The unripe female gonad is cream in colour and coarsely granular. The capsule gland is small and blotchy creamish-pink. The fully ripe condition is indicated by a finely granular, creamish-yellow or orange gonad, and a large white capsule gland.

The adults move down the shore in preparation for egg-laying which usually takes place near low water mark of spring tides (Moore 1938, Fretter and Graham 1962). If conditions are unsuitable at the low water spring tide mark the adults will merely move down to the lowest suitable level.

Crothers (1966) states that Nucella breeds all the year round in the Dale area, but that most capsules are laid in February and March (Crothers 1974). Feare (1969) reported spawning in April and May, and in 1967 a second spawning in August.

The egg capsules are vase-shaped and approximately 8 mm high and contain several hundred eggs embedded in an albuminous fluid. Crothers (1974) reported that the young Nucella escape from the egg cases after two or three months, whilst Connell (1961) records four months. There is no planktonic or other dispersal stage in the life cycle, the veliger stage taking place within the egg capsule. No-one has recorded the number of capsules laid per female. The majority of the eggs are used as food by the few developing protoconchs. The number of protoconchs released per capsule varies in the literature. Colton (1916) found on average 12, Pelseneer (1935) 15 ranging from 6 to 31, Feare (1969) 22 ranging from 13 to 36, and Crothers (1974) 10 to 12. Feare (1969) found that wherever capsules were permanently immersed in sea water 100% of the egg capsules hatched, but in situations which dried at low water hatching success varied between 0% at M.T.L. and 57% at M.L.W.N.

Materials and method

The adults collected each month (see page 40) were sexed and the sex ratio determined. Also the gonad state of the adults was recorded. Each month the gonads of these adults were dissected out and weighed. The gonad weights were expressed as a percentage of the flesh weight. The length of the dog-whelks in the study area was measured each month (see page 40) and their flesh weights obtained by substituting the shell lengths in the regression equations, for flesh weight on shell length (Table 15). Thus as the gonad weights were expressed as a percentage of the flesh weight the gonad weight for the study area was easily calculated. The gonad weights were converted to calories using the calorific values determined each month from dry weight samples of the gonads, using the Phillipson micro-bomb calorimeter.

The dates of winter and summer aggregations and time of appearance of the first egg capsules were recorded.

Results

The sex ratio was 56 males : 44 females. This was not statistically different from a 50 : 50 ratio.

The male and female gonads began to develop in December and were fully ripe by the end of February. Spawning animals were observed in early March and the gonads had reverted back to their inactive stage by the end of April. The gonads began developing again in mid-July and were fully ripe by the beginning of August. The animals spawned in early August and the gonads had reverted back to their inactive stage by the end of August (Tables 23 and 24).

The inactive gonad weight was 13% of the flesh weight, while when mature the male gonad was 22% and the female 22.7% (Table 25).

The calorific values of the ripe male gonads were 4.85 ± 0.11 Kcals/g or 5.41 ± 0.12 Kcals/ash free g, and the female gonads 4.93 ± 0.03 Kcals/g or 5.50 ± 0.03 Kcals/g ash free.

The gamete production was determined as the difference in weight of the gonad when mature compared to when inactive. This was determined for the adults in early March and August. The gamete production for the study area in March was 4.27 Kcals and in August was 3.88 Kcals which gave an annual total of 8.15 Kcals.

Discussion

The sex ratio (56♂ : 44♀) was not statistically different from a 50 : 50 ratio. Moore (1938) found that females outnumbered males (58 : 42), while Feare (1969) agreed with this study (54♂ : 46♀). Feare (1969) found that the proportion of females increased with age which was thought to be due to differential mortality of the sexes.

Table 23 *Nucella lapillus*: External appearance of the male gonad. Each category expressed as a percentage of the total: G, green; Y, yellow; O, orange; R, red; B, brown.

Month	Gonad colour				Ripe seminiferous tubules visible
	G-Y	Y-O	O-R	R-B	
January		10	85	5	90
February			15	85	100
March			20	80	100
April		20	60	20	60
May	10	75	15		
June	75	25			
early July	25	75			
late July		10	80	10	90
early August			20	80	100
late August		30	60	10	70
September	10	90			
October	80	20			
November	25	75			
December		40	60		

Table 24 *Nucella lapillus*: External appearance of the female gonad. Each category expressed as a percentage of the total: C, cream; O, orange.

Month	Gonad colour C	C-O	O
January		20	80
February			100
March			100
April	100		
May	80	20	
June		100	
early July		20	80
late July			100
early August			100
late August	100		
September	85	15	
October	60	40	
November	10	90	
December	10	80	10

Table 25 *Nucella lapillus*: Gonad weight expressed as a percentage of the flesh weight.

Male Gonad colour	% weight	Female Gonad colour	% weight
G-Y	12.9	Y	12.9
Y-O	12.9		
O-R	16.7	Y-O	17.0
R-B	22.0	O	22.7

The adult aggregations and spawning occurred on the M.L.W.N. ledge in the pools under the fucoid cover. The shore below this ledge consisted of boulders thickly covered in fucoids and obviously was not suitable for spawning. The adults aggregated in crevices and pools from the end of November until the end of March and again from the end of July to mid-August. The gonads were ripe in mid-February and at the end of July. Egg cases were first observed on the first of March and August. The ripe gonad weight of males was 22% and of females 24% of the flesh weight. Fretter and Graham (1962) state that the ripe gonad of the female may attain one-quarter of the body weight of the animal.

In one crevice 70 egg cases were deposited where 35 adults had aggregated for the winter. Therefore 4.7 egg cases per female were laid, provided the sex ratio was typical. If 4.7 egg cases per female was typical, then in the study area 98 were deposited in March (21 females present) and 75 deposited in August (16 females present). If 12 protoconchs hatch per egg case (the average number recorded by previous workers) then 1,179 hatched in July and 899 in November. If the number of summer and winter group juveniles surviving the first year are extrapolated back to the time of hatching, using the calculated mortality value (see page 51), the number of summer hatching juveniles would be 1,152 which is very similar to that calculated from the egg cases (1,171). However the number of winter hatching juveniles would be 1,414 which is 1½ times that estimated from the egg cases (899). Perhaps in the summer more egg cases per female were laid, which would be 7.4. Though the gonad weight as a percentage of the flesh in August and March was similar, the gonad in August was approximately 14% heavier than in March. This was because in the summer the somatic tissue was heavier than in March when the adults had not fed for nearly four months. This 14% increase in gonad weight would be unlikely to produce a 36% increase in the number of egg cases deposited. Possibly a higher number of protoconchs hatched per egg case in the autumn.

CHAPTER 4

RESPIRATION

Introduction

Since it is impractical to measure the energy lost through metabolic activities in poikilotherms by direct calorimetry, the indirect method of converting respiration into heat output by application of an oxycalorific coefficient must be used. The oxycalorific coefficient represents the heat released when 1 mg of oxygen is used to oxidize material which the animal is metabolizing. Ivlev (1935) calculated oxycalorific coefficients of 3.305, 3.280 and 3.529 for protein, fat and carbohydrate respectively, with a mean of 3.380. Consequently the general oxycalorific coefficient of 3.38 cal/mg of oxygen or 4.83 cals/ml of oxygen at N.T.P. may be used to convert population respiration rates into metabolic heat loss without introducing large errors.

The relationship between oxygen consumption and body weight in animals belonging to the same species can be described by the formula

$$Qo_2 = a.W^b$$

where a is the oxygen consumption per hour of an individual whose weight equals unity, b shows the degree of dependence of metabolic intensity upon the weight. Zeuthen (1953) found an average value of 0.75 for b in poikilotherms and Hemmingsen (1960) in a very extensive survey of literature also found a slope of 0.75.

Materials and method

Aquatic: The animals were collected from the shore half an hour before immersion by the tide. All animals were collected from the study ledge. In the laboratory the animals were immediately placed in the respiratory chambers (500 ml chambers for the limpets and 250 ml for the dog-whelks and littorinids). The chambers were glass jars with airtight screw tops. The chambers were kept in a constant temperature room at the ambient sea water temperature at Derbyhaven. At the time of tidal immersion of the study ledge the chambers were filled with sea water and sealed for six hours. The sea water was obtained directly from the sea via the sea water supply system of the building and left to stand in the constant temperature room for 12 hours before use. Thus the temperature of the sea water when used will be that of the room. Samples of this sea water were taken prior to and after the experiments and the oxygen content determined by the micro-Winkler technique. The oxygen content of the respiratory chambers was also determined after the six hour period. Thus the difference between the control sea water and the respiratory chamber water enabled the oxygen uptake of that animal to be calculated. At least one batch of twelve animals of each species was measured each month.

Aerial: The animals were collected from the study ledge while immersed and kept immersed until the laboratory was reached. At the time when the ledge became uncovered by the tide the animals were placed in the respiratory chambers at the ambient field air temperature. The limpets were placed into a constant pressure respirometer chamber (Davies 1966 modification of Scholander 1942 for medium sized animals) and the littorinids and dog-whelks in the Gilson respirometer chambers (see appendix). The oxygen uptake was recorded for six hours at half-hour intervals. Ten to twelve animals of each species were measured each month.

Calculations: As mentioned earlier, an exponential relationship exists between body weight and oxygen uptake

$$O_2 = aW^b \qquad (1)$$

Logarithmic transformation yields a linear relationship

$$\log O_2 = \log a + b \log W \qquad (2)$$

The regression of log oxygen uptake on log weight, i.e. equation (2), was calculated for each batch of experimental animals.

A model combining the temperature and size was constructed by plotting the regression intercept (a) and slope (b) for the fitted equations (i.e. equation 2) at the experimental temperatures against the experimental temperature (T) in °C. The linear regressions yield the following equations :

$$a = x + yT \qquad (3)$$

$$b = x_1 + y_1 T$$

By substituting the value for a and b in equation 3 for a and b in equation 1 the following relationship was determined :

$$O_2 = (x + yT)\, W^{(x_1 + y_1 T)}$$

For each month the average sea water temperature was substituted for (T) in °C in the derived model, which enabled the intercept (a) and slope (b) to be calculated for a regression of log oxygen uptake on log flesh dry weight for that month. Each month all the limpets in the quadrats were measured and their corresponding dry flesh weights calculated from regression equations (Table 4). The flesh dry weights of the limpets were substituted in that month's calculated regression equation and the oxygen uptake derived.

The study ledge was at a mid-tidal level on the shore (Fig. 2) and therefore each day will be immersed and exposed by the tide for 12 hours on average. Thus in calculating the total monthly aerial and aquatic consumption the total time was partitioned equally between the two. The oxygen consumption was corrected by a factor for activity. The application of the correction factor is discussed fully later on.

Results

The parameters for the regression equation (equation 2) are given in tables 26 to 31 inclusive.

The derived models are :

Patella vulgata

Aerial: $O_2 = (21.87 + 5.65\,T)\,W^{(0.7483 - 0.0036\,T)}$

Aquatic: $O_2 = (44.14 + 10.25\,T)\,W^{(0.7147 +).0037\,T)}$

Littorina littoralis –

Aerial: $0_2 = (-17.32 + 25.67\,T)\,W^{(0.60 + 0.0138\,T)}$

Aquatic: $0_2 = (43.40 + 14.84\,T)\,W^{(0.8256 - 0.0023\,T)}$

Nucella lapillus

Aerial: $0_2 = (57.07 + 4.86\,T)\,W^{(0.9488 - 0.0152\,T)}$

Aquatic: $0_2 = (50.66 + 11.18\,T)\,W^{(0.8127 - 0.0039\,T)}$

These regression equations were used to calculate the monthly oxygen consumption for the study populations (Tables 32 to 37 inclusive).

Discussion

The laboratory measurement of aquatic and aerial oxygen consumption coincided with the respective times of immersion and emersion by the tide. *P. vulgata* and *N. lapillus* showed definite tidal rhythms in aerial oxygen consumption. The oxygen consumption decreased at the beginning of the experiment to reach a minimum value around the time of low water, and then started to increase about an hour before the expected time of tidal immersion in the field. There was probably an aquatic tidal rhythm, but due to the technique for measuring the oxygen consumption it was not conclusively observed. Gompel (1937) observed that oxygen consumption in *P. vulgata* was maximal at high and minimal at low tide. Sandeen, Stephens and Brown (1954) described a persistent diurnal and tidal rhythm of consumption in *Littorina littorea* and *Urosalpinx cinerea*. Sandison (1966) observed that when *Littorina saxatilis* was placed in water the respiratory rate was influenced by a diurnal rhythm. *Littorina littorea* showed a tidal cycle in water and a diurnal rhythm in air. It would therefore appear that rhythms in oxygen consumption are not uncommon in intertidal gastropods.

Thus to observe the true aerial and aquatic oxygen consumption one must, as in this study, measure them at the times when these conditions occur in the field, and for the full periods of immersion and emersion. This has not usually been the case in most studies, which have neglected to correlate observations with tidal rhythms, and have used periods of observations often much shorter than the periods of immersion and emersion of the animal in the field.

In many studies the animals have often been collected and then left in the laboratory acclimating for several days before the experiment. In this study the measurement of oxygen consumption began within an hour of collection. There was no need for temperature acclimation as the respiratory chambers were kept at the ambient field temperature. It was observed early on in this study that if the animals were left in the laboratory for more than a day the tidal rhythm was diminished or lost. This factor could explain why so few respiratory rhythms have been observed during the many respiratory studies of intertidal animals.

No aerial or aquatic rhythm was observed in the respiration of L. littoralis, an absence which Sandison (1966) had previously noted. The tidal respiratory rhythms of P. vulgata and N. lapillus are adaptive since both show tidal rhythms of activity; limpets and dog-whelks only commence movement when spray continually reaches them and terminate it before being uncovered (Hartnoll and Wright, in press). The littorinids became active at the onset of water coverage of the algal fronds, but they remained active following the ebbing tide, being particularly noticeable on the surface of the algal clumps. Activity ceased only as the substratum dried (Bray 1974). Thus activity depends on the drying of the algae not the tidal state, and a tidal rhythm in respiration would not be adaptive.

The respiratory rates of these three species cannot be directly compared because of the different sizes of the species and the allometric relationship which exists between body weight and respiratory rate. This relationship has been expressed by Zeuthen (1953) and Hemmingsen (1960) in a wide range of poikilotherms to be, $b = 0.75$, in the equation

$$O_2 = aW^b$$

When the respiratory rates in water of these three species were plotted on double logarithmic paper against the average body weight of a mature animal of each species, and the time for $b = 0.75$ for respiration was drawn, it was found that the respiratory rate of *P. vulgata*, *L. littoralis* and *N. lapillus* lay remarkably close to the line (Fig. 20); the regression line for these points gave a slope (b) of 0.72. In other words, when the size difference between the species was taken into account the graph showed there was no difference in the aquatic respiratory rates of *P. vulgata*, *L. littoralis* and *N. lapillus*.

The respiratory rates in air did not fit a line with a slope of 0.75. When such a line is drawn through an average sized *P. vulgata* (broken line in Fig. 20) the respiratory rate of *N. lapillus* was 1⅓ times higher and *L. littoralis* 3⅓ times higher than the corresponding points on the line. The relatively higher rates of oxygen consumption of *L. littoralis* and *N. lapillus* were related to their behaviour. *P. vulgata* ceases movement one or two hours before being uncovered by the tide (Hartnoll and Wright, in press) and will be completely inactive when exposed. *N. lapillus* ceases movement when uncovered by the tide, but will continue to feed if so doing, and therefore will not be completely inactive when exposed. *L. littoralis* was seen to keep the operculum open and even to crawl when exposed to air and continue feeding until the algae dried, so it will therefore be in a semi-active state when uncovered.

The coefficient (b) for aquatic and aerial respiration was close to 0.75 for the species individually. The aquatic coefficients were 0.75, 0.80 and 0.77, and the aerial 0.71, 0.74 and 0.78 for *P. vulgata*, *L. littoralis* and *N. lapillus* respectively.

Errors are involved in extrapolating respiration rates measured in the laboratory to the field situation where conditions may be quite different. It is difficult to know how much more or less active an animal is in its natural habitat than in the respirometer. Several authors have measured respiration rates of the animals at rest and multiplied by a factor of two to account for activity in the field (Brody, Proctor and Ashworth 1934, Odum, Connell and Davenport 1962, Winberg 1956, Mann 1964 & 1965, Carefoot 1967 and Trevallion 1971). The animals were probably at rest when measured in the laboratory as little movement was observed. P. vulgata was only observed to be active in the field when foraging; this only took place when immersed in daylight (Hartnoll and Wright, in press) and an arbitrary correction of times two was applied for these periods. The corrected yearly aquatic oxygen consumption was 433.8 Kcals and 458.2 Kcals in 1974 and 1975 respectively. The aerial consumption was 144.5 and 151.8 Kcals in 1974 and 1975 respectively. Therefore the total oxygen consumption was 578.3 and 610.0 Kcals in 1974 and 1975 respectively.

L. littoralis is active when immersed, so the aquatic oxygen consumption was corrected for by a factor of times two. Thus the aquatic consumption was 67.73 Kcals /Kg dry weight fucoid. The animals may continue feeding when exposed but rarely move, so the aerial consumption measured in the laboratory was probably representative of field consumption. The aerial consumption was 48.8 Kcals and the yearly oxygen consumption 116.53 Kcals/Kg dry weight fucoid.

N. lapillus oxygen consumption was corrected by a factor of two for the periods when feeding. The percentage number of animals and periods of feeding varied with age and season (Table 50). The corrected yearly aquatic and aerial oxygen consumption were 135.6 and 82.4 Kcals respectively, giving a yearly total of 218 Kcals.

Sandison (1966) measured the oxygen consumption of L. littoralis and N. lapillus at 18°C in air and water. He found that a littorinid weighing 0.236 g wet weight in water consumed 98.1 μl/g/hr, and an animal weighing 0.217 g wet weight in air consumed 217 μl/g/hr. Using my aerial and aquatic models, the oxygen consumption of these specimens was estimated as 116.4 μl and 230.8 μl/g/hr in water and air respectively. Errors will have arisen in converting his wet weights to dry weights, and also 18°C is outside the temperature range for which the models were constructed. However Sandison's (1966) oxygen consumption estimates, especially in air, are similar to those determined here.

Sandison (1966) found that a dog-whelk weighing 1.091 g wet weight in air measured 109.8 µl/g/hr and an animal weighing 1.24 g wet weight in water used 59.2 µl/g/hr. Utilizing my aerial and aquatic models, the oxygen consumption of these specimens was estimated as 58,7 µl and 75.5 µl/g/hr in air and water respectively. Again Sandison's oxygen consumptions are similar to my figures.

Table 26 *Patella vulgata*: Parameters for the regression of log aerial oxygen consumption in μls/hour on dry flesh weight in g.

Temperature (°C)	Date	Coefficient of correlation	Intercept	Slope
15.90	1.10.75	97.83	2.0805	0.7399
15.30	17.7.75	89.22	2.0153	0.6537
14.90	1.9.75	94.21	2.0144	0.6882
13.25	30.6.75	96.49	1.9928	0.7079
13.25	17.6.75	98.11	1.9826	0.7018
11.30	30.10.75	99.01	1.8970	0.7033
9.20	19.5.75	95.11	1.8992	0.6942
7.70	15.12.75	97.71	1.8214	0.7176
7.50	21.4.75	96.78	1.7872	0.7156
6.00	21.2.75	97.77	1.7263	0.7263
5.00	5.3.75	99.04	1.7308	0.7526

Table 27 *Patella vulgata*: Parameters for the regression of log aquatic oxygen consumption in μls/hour on dry flesh weight in g.

Temperature (°C)	Date	Coefficient of correlation	Intercept	Slope
15.00	29.10.75	98.11	2.2961	0.7619
14.70	5.7.75	96.12	2.2795	0.7717
14.00	14.7.75	99.01	2.2843	0.7529
13.10	22.10.75	98.77	2.2258	0.7514
11.90	22.10.74	97.21	2.2508	0.7722
11.90	26.6.75	94.91	2.2108	0.7429
11.40	19.11.75	99.09	2.2087	0.7525
10.00	24.12.75	87.64	2.1669	0.7479
9.40	30.5.75	85.92	2.1470	0.7474
9.20	3.1.75	97.40	2.1622	0.7471
8.40	31.1.75	97.59	2.1065	0.7371
8.40	28.4.75	98.18	2.1393	0.7290
7.10	18.3.75	98.93	2.0258	0.7478

Table 28 Littorina littoralis: Parameters for the regression of log aquatic oxygen consumption in μls/hour on dry flesh weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.30	10.8.75	0.9216	2.3629	0.7554
14.80	27.7.75	0.9640	2.3646	0.7659
14.00	8.9.75	0.9892	2.3396	0.7595
13.50	24.9.74	0.9899	2.2529	0.7372
13.00	1.10.74	0.9714	2.3884	0.8338
12.60	28.6.75	0.9428	2.4749	0.8826
10.75	23.5.75	0.9901	2.3576	0.7728
10.60	19.11.74	0.9211	2.3430	0.8424
10.00	2.12.74	0.9122	2.4234	0.9030
9.90	5.12.74	0.9915	2.1956	0.7672
9.50	10.5.75	0.9715	2.3283	0.8587
7.80	27.1.75	0.9827	2.1478	0.7620
7.30	15.2.75	0.9774	2.0990	0.7420
7.10	11.3.75	0.9783	2.1706	0.8023

Table 29 Littorina littoralis: Parameters for the regression of log aerial oxygen consumption in μls/hour on dry flesh weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.75	29.6.75	0.9127	2.6327	0.8070
14.40	25.6.75	0.9838	2.4719	0.7382
14.50	30.8.75	0.9722	2.5212	0.7174
14.00	11.9.75	0.9649	2.7860	1.0053
14.00	10.9.75	0.9651	2.6930	0.9242
11.00	7.6.75	0.9821	2.3472	0.7008
10.00	24.5.75	0.9878	2.1987	0.5958
10.00	25.5.75	0.9863	2.0325	0.4532
10.00	7.10.74	0.9902	2.6376	0.9233
9.75	20.5.75	0.9316	2.3841	0.7640
7.70	4.4.75	0.9525	2.4144	0.8563
7.70	11.12.74	0.9600	2.1151	0.6149
7.50	15.1.75	0.9794	2.0792	0.6331
5.00	5.3.75	0.9853	2.2345	0.7814

Table 30 *Nucella lapillus*: Parameters for the regression of log aerial oxygen consumption in μls/hour on dry flesh weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.75	1.9.75	0.9372	2.0991	0.6828
14.90	23.6.75	0.9851	2.0532	0.6990
14.50	26.8.75	0.9462	2.0417	0.6839
14.00	12.9.75	0.9729	1.9658	0.6633
14.00	15.9.75	0.9634	2.2965	0.9288
11.00	10.6.75	0.9710	2.1122	0.8203
10.00	25.5.75	0.9889	1.9632	0.7061
10.00	11.10.74	0.9773	2.0550	0.7987
9.75	23.5.75	0.9754	2.0535	0.8040
7.70	5.4.75	0.9765	1.9799	0.8059
7.70	14.12.74	0.9238	1.9971	0.8480
7.00	21.1.75	0.9316	2.0379	0.8477
5.00	8.3.75	0.9517	1.9370	0.8881

Table 31 *Nucella lapillus*: Parameters for the regression of log aquatic oxygen consumption in μls/hour on dry flesh weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.30	11.8.75	0.9273	2.3202	0.7156
14.80	28.7.75	0.9718	2.3017	0.7411
14.00	7.9.75	0.9802	2.2895	0.7665
13.50	23.9.74	0.9611	2.2292	0.7081
13.00	5.10.74	0.9489	2.0731	0.6412
12.60	25.6.75	0.9514	2.2923	0.7764
10.75	24.5.75	0.9600	2.4038	0.9085
10.60	21.11.74	0.9525	2.3357	0.8628
10.00	3.12.74	0.9417	2.3582	0.8301
9.90	9.12.74	0.9825	2.2624	0.8681
9.50	11.5.75	0.9899	2.2793	0.8225
7.80	28.1.75	0.9205	2.0655	0.7010
7.30	13.2.75	0.9426	1.9806	0.6985
7.10	9.3.75	0.9596	2.0481	0.7196

Table 32 *Patella vulgata*: Parameters for the regression of log aquatic oxygen consumption in μls/hour on flesh dry weight in g. and the aquatic oxygen consumption each month of the quadrats population.

Month	Temperature (°C)	Intercept	Slope	O_2 consumption (in Kcals)	Consumption corrected for activity
1974					
March	7.8	2.0937	0.7396	16.78	25.18
April	8.4	2.1144	0.7415	19.82	31.38
May	9.7	2.1570	0.7454	24.35	40.59
June	11.7	2.2171	0.7506	26.17	44.71
July	13.4	2.2611	0.7566	32.40	53.99
August	14.3	2.2803	0.7604	33.11	53.81
September	13.6	2.2655	0.7576	31.65	48.79
October	11.6	2.2140	0.7550	24.07	35.10
November	10.6	2.1852	0.7514	23.62	32.48
December	9.2	2.1387	0.7473	17.42	23.22
1975					
January	8.4	2.1104	0.7440	16.65	22.89
February	7.5	2.0743	0.7410	15.30	21.67
March	7.4	2.0727	0.7356	16.91	25.37
April	8.3	2.1089	0.7391	20.67	32.73
May	9.4	2.1481	0.7436	25.14	41.91
June	11.9	2.2225	0.7536	30.64	52.34
July	14.3	2.2813	0.7584	32.60	54.33
August	15.0	2.2971	0.7606	36.48	59.29
September	14.3	2.2813	0.7584	33.03	53.68
October	13.0	2.2495	0.7586	27.96	40.78
November	11.3	2.2048	0.7545	21.59	29.68
December	10.0	2.1659	0.7523	19.04	25.38
1976					
January	8.9	2.1315	0.7411	16.47	22.65
February	7.2	2.0615	0.7399	14.15	20.05

Table 33 *Patella vulgata*: Parameters for the regression of log aerial oxygen consumption in µls/hour on flesh dry weight in g. and the aerial oxygen consumption each month of the quadrats population.

Month	Temperature (°C)	Intercept	Slope	O_2 consumption in Kcals
1974				
March	6.1	1.7509	0.7263	7.85
April	8.1	1.8301	0.7192	10.82
May	10.0	1.8941	0.7094	13.57
June	13.0	1.9791	0.6997	15.48
July	13.8	1.9969	0.6975	17.84
August	14.0	2.0042	0.6979	17.78
September	11.9	1.9526	0.7030	13.32
October	8.8	1.8624	0.7141	10.92
November	7.5	1.8147	0.7200	10.16
December	8.2	1.8413	0.7167	11.20
1975				
January	7.3	1.8066	0.7210	8.35
February	6.0	1.7480	0.7283	7.19
March	5.5	1.7220	0.7315	7.60
April	8.0	1.8340	0.7177	11.00
May	9.4	1.8807	0.7108	13.77
June	13.2	1.9836	0.6991	17.81
July	15.4	2.0297	0.6935	19.80
August	15.9	2.0392	0.6922	20.44
September	12.5	1.9674	0.7012	16.27
October	11.3	1.9372	0.7049	13.82
November	8.0	1.8340	0.7177	9.34
December	7.4	1.8107	0.7205	8.57
1976				
January	7.1	1.7983	0.7221	7.78
February	4.5	1.6620	0.7389	5.63

Table 34 **Littorina littoralis**: Parameters for the regression of log aquatic oxygen consumption in μls/hour on flesh dry weight in g. and the aquatic oxygen consumption each month per kilogram dry weight of fucoid.

Month	Temperature (°C)	Intercept	Slope	O_2 consumption in Kcals
January	8.4	2.2255	0.8064	2.38
February	7.5	2.1892	0.8027	1.98
March	7.4	2.1856	0.8032	2.17
April	8.3	2.2206	0.8017	2.29
May	9.4	2.2600	0.8012	2.59
June	11.9	2.3329	0.7987	2.99
July	14.3	2.3905	0.7975	3.55
August	15.0	2.4050	0.7968	3.68
September	14.3	2.3905	0.7975	3.43
October	13.0	2.3602	0.7978	3.29
November	11.3	2.3167	0.7997	2.87
December	10.0	2.2791	0.8005	2.72

Table 35 **Littorina littoralis**: Parameters for the regression of log aerial oxygen consumption in μls/hour on flesh dry weight in g. and the aerial oxygen consumption each month per kilogram dry weight of fucoid.

Month	Temperature (°C)	Intercept	Slope	O_2 consumption in Kcals
January	7.3	2.2306	0.7007	3.38
February	6.0	2.1354	0.6828	2.68
March	5.5	2.0967	0.6759	2.80
April	8.0	2.2717	0.7104	3.48
May	9.4	2.3470	0.7297	4.01
June	13.2	2.5055	0.7828	4.90
July	15.4	2.5775	0.8125	5.64
August	15.9	2.5924	0.8194	5.76
September	12.5	2.4801	0.7725	4.72
October	11.3	2.4330	0.7559	4.55
November	8.0	2.2717	0.7104	3.48
December	7.4	2.2353	0.7021	3.41

Table 36 *Nucella lapillus*: Parameters for the regression of log aerial oxygen consumption in ls/hour on flesh dry weight in g. and the aerial oxygen consumption each month of the population in the study area.

Month	Temperature (°C)	Intercept	Slope	O_2 consumption (in Kcals)	Consumption corrected for activity
January	7.3	1.9665	0.8378	3.68	4.51
February	6.0	1.9358	0.8576	2.72	2.97
March	5.5	1.9111	0.8652	2.61	4.01
April	8.0	1.9855	0.8272	3.01	5.17
May	9.4	2.0178	0.8059	3.53	6.47
June	13.2	2.0859	0.7481	4.40	7.71
July	15.4	2.1172	0.7147	5.93	11.00
August	15.9	2.1280	0.7071	6.35	10.62
September	12.5	2.0738	0.7583	5.64	10.50
October	11.3	2.0553	0.7770	5.15	8.46
November	8.0	1.9855	0.8272	3.82	6.07
December	7.4	1.9699	0.8363	3.91	4.92

Table 37 *Nucella lapillus*: Parameters for the regression of log aquatic oxygen consumption in ls/hour on flesh dry weight in g. and the aquatic oxygen consumption each month of the population in the study area.

Month	Temperature (°C)	Intercept	Slope	O_2 consumption (in Kcals)	Consumption corrected for activity
January	8.4	2.1602	0.7799	6.19	7.60
February	7.5	2.1259	0.7834	4.85	5.29
March	7.4	2.1226	0.7838	4.89	7.52
April	8.3	2.1565	0.7803	4.74	8.14
May	9.4	2.1944	0.7760	5.42	9.94
June	11.9	2.2657	0.7662	6.70	11.74
July	14.3	2.3218	0.7569	8.81	16.32
August	15.0	2.3365	0.7542	9.54	15.94
September	14.3	2.3218	0.7569	9.36	17.42
October	13.0	2.2934	0.7620	8.83	14.52
November	11.28	2.2496	0.7687	7.48	11.87
December	10.0	2.2135	0.7737	7.41	9.32

CHAPTER 5

INGESTION AND EGESTION

1. General Introduction

This chapter discusses the measurement of ingestion, C, i.e. the energy content of the food consumed by the population, and egestion, F + U, i.e. F is the energy leaving the population as faeces and U is the energy lost via excreted urine or other exudates.

The ingestion of the three species was determined by measuring the food intake of animals in known time periods. The egestion was measured at the same time by collecting the faeces and analysing the sea water for urine production.

2. Patella vulgata

Introduction

Hartnoll and Wright (in press) determined that in two populations of Patella vulgata (one population was at Derbyhaven on the study ledge) in the Isle of Man foraging activity is restricted to daytime high waters with about 75% of the population foraging on any one day. Movement commences as the tide covers the limpets, and they travel an average 0.4 m from their home sites to which they return at least an hour before the falling tide exposes them again. This behaviour contrasts with that of the same species in Alderney, where foraging is limited to nocturnal low waters; there is possibly a geographical trend in behaviour.

Patella vulgata browses on detritus and algal growth. When feeding it moves systematically around its home rasping with the radula anything which it happens to meet, and consequently there is a considerable variation in the diet. Individuals living in the Balanus zone collect diatoms, silt and debris, whereas others living amongst Enteromorpha, Ascophyllum and Fucus fill their gut with algae sporelings (Fretter and Graham 1962). The larger algae can be utilized as food since the limpet has enzymes capable of digesting laminarin (Dr. V.C. Barry, quoted by Jones 1948) and fucoidin and of de-esterifying their carbohydrate sulphates (Dodgson and Spencer 1954).

Moore (1938) made the only quantitative observations on limpet feeding in his study of Patella vulgata. He estimated that during the first year of life an area of about 75 sq cm is required to provide sufficient food for the maintenance of each c.c. of limpet. He calculated this from regions covered by a thick felt of Enteromorpha sp., Porphyra umbilicalis and other algae.

The faeces of P. vulgata are in the form of cylindrical pellets. Moore (1931) observed that the pellets are normally composed of fairly coarse detritus with some diatom skeletons and numerous algal fragments. The pellets from an animal 2.5 cm long average 0.5 cm in diameter and are usually 0.5 to 1 cm in length. The greater part of the nitrogen excreted in Patella is in the form of ammonia (Fretter and Graham 1962). There have been no previous quantitative data on faecal or urine production.

Materials and method

Ordinary house slates (50 cm x 25 cm) were placed in wire baskets and bolted onto the ledge. The baskets were to prevent limpets moving on or off the slate. The slates were left on the ledge until covered with an algal mat. Then a limpet was removed from the surrounding area and placed on the slate. The area grazed after one immersion of the tide, left as a clear track in the algal mat, was estimated. The algal density (g. dry wt/m^2) of the rest of the mat was determined and thus the dry weight of algae in the grazed area, i.e. the algae ingested, could be calculated.

Other slates, when covered in an algal mat, were brought into the laboratory and placed in tanks kept at the ambient field temperature. A limpet was placed on each slate and as before the area grazed was recorded. The faeces produced were collected and dry weights determined.

The percentage assimilation can be calculated indirectly by the ash ratio method of Conover (1966). This method requires neither the quantitative recovery of faeces nor knowledge of the amount of food eaten. The method depends on the assumption that only the organic component of food is significantly affected by the digestive process. If this assumption is correct, it is necessary only to obtain the ratio of ash free dry weight to dry weight (fraction of organic matter) for a sample of food and a sample of faeces to calculate percentage of assimilation, using the equation

$$\text{Assimilation efficiency} = \frac{(F - E)}{(1 - E)\,F} \times 100$$

where F and E are the organic fraction of the food and faeces respectively. A sample of the mat was taken, which consisted largely of Enteromorpha species. The faeces were collected from the limpets on the slates. The dry weight and ash content of the mat and faeces were determined and the assimilation efficiency calculated by the ash ratio method of Conover.

The ammonia produced was collected by setting up the animals in the respiratory chambers, following the procedure used for measuring aquatic oxygen consumption. Instead of using the micro-Winkler technique, the Berthelot procedure was followed (as described by Solórzano 1969 and Harwood and Huyser 1970). The ammonia production (g.) was converted to calories using the Brafield and Soloman (1972) coefficient of 68.9 Kcals/mol.

Results

The ingestion by experimental animals, during one daylight tidal immersion, on the shore in June, August and September is shown in Table 38.

The relationship between ingestion (I) and body weight (W) in animals belonging to the same species can be described by the formula

$$I = aW^b$$

where a is the ingestion per day of an individual whose weight equals unity, b shows the degree of dependence of ingestion upon the weight. Logarithmic transformation yields a linear relationship

$$\log I = \log a + b \log W$$

Regressions of log ingestion on log dry body weight were calculated for June, August and September (Table 39) using the ingestions measured on the shore

Table 38 Patella vulgata: The ingestion per daylight tidal immersion of animals on the shore in June, August and September.

Month	Length (mm)	Dry weight (g.)	Ingestion (cals)	Ingestion (cals. g^{-1} dry wt. animal)
June	51.33	1.6784	191	114
	50.44	1.7892	164	91
	45.68	1.0053	124	123
	44.50	1.1121	133	120
	35.96	0.4389	42	96
	23.70	0.0922	14	148
August	53.61	2.2981	274	119
	51.41	1.9031	243	128
	46.04	1.4532	112	77
	43.79	1.2147	103	85
	40.62	0.6499	89	137
	38.67	0.6254	87	140
	31.26	0.2431	37	150
	21.52	0.0618	6	99
September	53.01	2.2268	228	102
	50.09	1.7241	165	96
	45.92	1.0762	99	92
	40.60	0.7342	63	86
	40.62	0.8357	94	113
	22.00	0.0624	7	119

Table 39 Patella vulgata: Parameters for the regression of log ingestion in cals/day on dry body weight in g. and the ingestion for June, August and September, and also estimates of annual ingestion for the quadrats population.

Month	Correlation coefficient	Intercept	Slope	Ingestion (Kcals)	Annual ingestion (Kcals)
June	0.9909	2.0433	0.9050	343.9	3,010
August	0.9791	2.0523	0.9743	349.6	2,702
September	0.9964	1.9946	0.9449	289.1	2,468

(Table 38). Each month all the limpets in the quadrats were measured and their corresponding dry flesh weights calculated from regressions (Table 4). The flesh dry weights of the limpets were substituted in that month's calculated regression and the ingestion derived. The ingestions for June, August and September were 343.9, 349.6 and 289.1 Kcals respectively (Table 39).

Three estimates of annual ingestion were calculated using the three monthly ingestion values. It was assumed for the estimation that the monthly ingestion as a proportion of the annual ingestion was in the same proportion as that monthly respiration (Tables 32 & 33) was of the annual respiration. This is a dubious assumption as feeding rate can depend on many factors other than simply respiration; however these estimates are of use (discussed later on). The three estimates of annual ingestion were 3,010, 2,702 and 2,468 Kcals calculated from the June, August and September monthly ingestions respectively.

The ingestion index is the daily ingestion in Kcals divided by the value of the flesh tissue in Kcals times 100. The daily ingestion indices for June, August and September were 2.49, 2.39 and 2.13 respectively. The index of daily ingestion was also calculated for the three estimates of annual ingestion and were 2.16, 1.93 and 1.77.

The calorific value of the limpet faeces was 0.94 ± 0.10 Kcals/g or 3.34 ± 0.36 Kcals/ash free g, as the ash content was 71.8%. The calorific value of the algal mat, washed free of particles, was 2.65 ± 0.09 Kcals/g or 4.42 ± 0.15 Kcals/ash free g, as the ash content was 40%. The ash content of the unwashed mat was 65%. The assimilation efficiency ratios calculated by the ash ratio method of Conover were 73.8 and 27.1% for the washed and unwashed mat respectively. The ingestion of the limpets during June, August and September have been calculated and therefore, using the calculated assimilation efficiencies, the faeces production of these months can be calculated. The faeces productions assuming an assimilation efficiency of

73.8% were 90, 91.5 and 75.7 Kcals for June, August and September respectively, but 251, 255 and 211 Kcals assuming a value of 27.1%. Also using the calculated assimilation efficiencies the faeces production can be calculated for the estimates of the yearly ingestions. The annual faeces productions if the assimilation efficiency was 73.8% were 788, 707 and 716 Kcals, while if it were 27.1% they become 2,194, 1,970 and 1,799 Kcals. The appropriate assimilation efficiency to use is discussed later.

It is assumed that an exponential relationship exists between body weight (W) and ammonia excretion (U):

$$U = aW^{b} \qquad (1)$$

where a is the ammonia production per day of an individual whose weight equals unity and b shows the degree of dependence of ammonia excretion upon the weight.

Logarithmic transformation yields a linear relationship:

$$\log U = \log a + b \log W \qquad (2)$$

A model combining the temperature and size was constructed by plotting the intercept (a) for the fitted equations at the experimental temperatures (Table 40) against the experimental temperature (T) in ^{o}C. The linear regression of these data yields the following equation:

$$a = 0.9382 + 0.1552\, T \qquad (3)$$

The slope (b) also varies with temperature, so the slope (b) for the fitted equations at the experimental temperatures (Table 40) was plotted against the experimental temperature (T) in ^{o}C. The linear regression of these data yields the following equation:

$$b = 0.4563 + 0.0201\, T \qquad (4)$$

By substituting the value for a in equation 3 for a in equation 1, and the value b in equation 4 for b in equation 1, the following relationship was derived:

$$U = (0.9382 + 0.1552\, T)\, W^{(0.4563 + 0.0201\, T)}$$

For each month the average sea water temperature was substituted for

Table 40 *Patella vulgata*: Parameters for the regression of log nitrogen excretion in g.N-NH_3/day on dry body weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.0	2.9.75	0.9834	0.5329	0.7608
13.5	22.10.75	0.9686	0.4493	0.7065
11.7	26.6.75	0.9109	0.4355	0.6970
8.9	2.2.75	0.9615	0.3788	0.6570
8.3	1.5.75	0.9733	0.4033	0.6741
7.4	1.4.75	0.9877	0.2596	0.5567

Table 41 *Patella vulgata*: Parameters for the regression of log nitrogen excretion in g.N-NH_3/day on dry body weight in g. and the nitrogen excretion each month of the quadrats population.

Month	Temperature (°C)	Intercept	Slope	N-NH_3 (Kcals/month)
1974				
March	7.8	0.3331	0.6128	0.12
April	8.4	0.3412	0.6269	0.14
May	9.7	0.3794	0.6564	0.18
June	11.7	0.4355	0.6970	0.21
July	13.4	0.4812	0.7278	0.27
August	14.3	0.5049	0.7432	0.25
September	13.6	0.4866	0.7313	0.20
October	11.6	0.4327	0.6950	0.18
November	10.6	0.4050	0.6753	0.18
December	9.2	0.3649	0.6454	0.12
1975				
January	8.4	0.3231	0.6122	0.12
February	7.5	0.3138	0.6045	0.12
March	7.4	0.3109	0.6020	0.11
April	8.3	0.3383	0.6246	0.14
May	9.4	0.3707	0.6499	0.19
June	11.9	0.4410	0.7008	0.24
July	14.3	0.5009	0.7432	0.28
August	15.0	0.5140	0.7546	0.29
September	14.3	0.5009	0.7432	0.27
October	13.0	0.4706	0.7208	0.22
November	11.3	0.4245	0.6893	0.16
December	10.0	0.3881	0.6629	0.14
1976				
January	8.9	0.3646	0.6452	0.11
February	7.2	0.3046	0.5968	0.10

(T) in $^{\circ}$C in the derived model which enabled the intercept (a) and slope (b) to be calculated for a regression equation, log ammonia excreted/log flesh dry weight, for that month (Table 41). Each month all the limpets in the quadrats were measured and their corresponding dry flesh weights calculated from regression equations (Table 4). The flesh dry weights of the limpets were substituted in that month's calculated regression equation and the ammonia excreted derived. The ammonia excreted varied from 0.1 Kcals/month in February 1976 to 0.29 Kcals/month in August 1975 (Table 41). The annual ammonia excreted for 1974 and 1975 was 2.08 and 2.25 Kcals respectively.

Discussion

Numerous problems were encountered in trying to measure assimilation. During the spring, autumn and winter of 1975 the slates were broken or washed away in storms before a sufficient algal mat was present. Thus ingestion was only measured in the summer months. The laboratory experiments failed as the limpets appeared not to feed and eventually died even though they were kept as near as possible to the ambient field conditions.

The ingestion for June and August was similar, 343.9 and 349.6 Kcals respectively, while for September the ingestion was lower, 289.1 Kcals. The average temperatures for June, August and September were 11.9, 15.0 and 14.3°C respectively. These data therefore do not show the expected relationship between ingestion and temperature, namely a corresponding increase in ingestion with increasing temperature and vice versa. However only six animals were observed in June and September and eight in August. The small number and variability of the measurements may have obscured the relationship or it may be that gonadal development influenced feeding. During June the animals were building up food stores. In August the gonads began developing and by September the gonadal development was well advanced. Perhaps during gonad development feeding is reduced. The increase in calorific value of the somatic tissue between October and November 1975, when the gonads were ripe, was much slower than that after spawning (Fig. 11).

Thus it can be assumed that ingestion was reduced during October and November. The calorific value of the somatic tissue decreased from August to October 1975, while the gonads increased in calorific value. Thus food stores from the somatic tissue were being transformed and assisting in gonad maturation. However it was not possible to detect whether ingestion was reduced. As the gonads mature they increase rapidly in size, and when ripe are up to 40% of the flesh weight (Table 19). Thus the possible expansion of the gut will be greatly reduced and this will probably reduce the ingestion rate.

The assimilation efficiency calculated by the ash-ratio method of Conover was 73.8% when the algal mat sample was washed and all the non-algal material, e.g. pieces of slate, removed. The percentage ash of the algal mat without washing was 65% compared to 40% when washed and gave an assimilation efficiency of 27.1%. Blackmore (1969) observed that the ratio of weed to rock in the limpet gut varied from 34.7% in August 1965 to 8.6% in February 1965. If this is correct then the true assimilation efficiency is likely to be nearer 27.1% than 73.8%. Hughes (1971) calculated a similar assimilation efficiency for the Keyhole limpet, Fissurella barbadensis, 33.6%. This animal has a similar feeding habit and ingests sand grains and rock particles (Ward 1967).

The ingestion index for June, August and September was 2.49, 2.39 and 2.13 respectively. The annual index values calculated on the basis of each of the foregoing were lower at 2.16, 1.93 and 1.77, giving an average of 1.95. The three months, June, August and September, will be months of high ingestion, while the annual value includes months of lower ingestion, as feeding is temperature dependent.

The ammonia excreted was 2.08 Kcals in 1974 and 2.25 Kcals in 1975. Ammonia excretion is negligible when compared to faeces production (i.e. 0.26 to 0.35% of faeces production).

3. Littorina littoralis

Introduction

The preference for Fucaceae as a food source is generally accepted (Barkmann1955, Bakker 1959 and Guiterman 1971) though Nicol (Guiterman 1971) reports Laminaria as a source of food for the animal on North Scottish coasts. Van Dongen (1956) has shown that L. littoralis is attracted by the scent of the Fucaceae from a distance of 1 m. The attraction is strongest to F. vesiculosus and least to F. serratus. Bray (1974) found that L. littoralis showed no difference in attraction to F. serratus, F. vesiculosus, F. spiralis or Ascophyllum nodosum. Also in this study the littorinias showed no preference between F. vesiculosus and F. serratus during the laboratory feeding experiments.

The faecal pellets are usually composed of algal fragments or else of detritus and diatom skeletons. The pellets are oval, of average length to breadth ratio 1.85, and from an animal 8.5 mm long about 0.31 mm in breadth (Moore 1931).

Materials and method

The food (F. serratus or F. vesiculosus) was collected from the shore and taken to the laboratory. The fucoid was shaken and excess water removed by blotting. Portions of the algae were weighed and placed into the feeding containers. The wet and dry weight of the remaining algae was determined. This enabled a wet : dry ratio of the algae to be calculated. Animals freshly collected from the shore were then added to the containers which were kept at the ambient field temperatures and tidal cycles of immersion and emersion for three or five days. The faeces produced were collected each day. When the experiments were terminated the dry weights of the animals were determined. The algae was shaken, blotted and the wet and dry weight determined. Knowing the wet to dry ratio of the algae prior to and after the experiment, any difference in the algal water content can be adjusted for and the amount of algae consumed calculated.

The sea water drained out of the feeding containers at the end of each immersion period was collected and analysed for ammonia following the Berthelot procedure. A sample of the sea water before each filling of the containers was also analysed for ammonia. The difference in the ammonia concentration of the sea water before and after the experiment enabled the ammonia production to be calculated.

The calorific value of *F. serratus* and *F. vesiculosus* was determined each month from dry weight samples of the fucoid, using the Phillipson micro-bomb calorimeter. The calorific value of dry weight samples of faeces were also determined.

Results

The ingestion rates of similar sized littorinids in the laboratory varied enormously, contrasting with the relatively steady faecal production rates. The weight of algae consumed compared to the weight in the feeding containers was very small. Therefore slight changes in the wet to dry ratio of the algae not accounted for prior to and after the experiment could have produced this variability. However the faecal production would not have been affected. The ingestion/faecal production ratio (1:1.8) was calculated from laboratory feeding experiments (Table 42). For each of the experimental temperatures a regression equation of faeces production against weight was calculated (Table 43).

The relationship between faecal production (F) and body weight (W) was

$$F = aW^b \qquad (1)$$

where a is the faeces production per day of an individual whose weight equals unity and b shows the degree of dependence of faeces production upon the weight.

Logarithmic transformation yields a linear relationship:

$$\log F = \log a + b \log W \qquad (2)$$

A model combining the temperature and size was constructed by plotting the intercept (a) for the fitted equations at the experimental temperatures

Table 42 *Littorina littoralis*: The ingestion, faeces production and the ingestion/faeces ratio measured in the laboratory.

Temperature (°C)	Date	Ingestion (C) (g)	Faeces (F) (g)	C/F
9.8	25.5.75	0.096	0.0672	1.43
10.0	2.6.75	0.3633	0.1892	1.92
10.0	6.6.75	0.1613	0.0972	1.66
14.3	19.10.75	0.4004	0.2064	1.44
15.2	23.9.75	0.7558	0.3705	2.04
			Average	1.80

Table 43 *Littorina littoralis*: Parameters for the regression of log faeces production in g/day on dry body weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.2	23.9.75	0.8911	-1.5817	0.9932
14.3	19.10.75	0.9423	-1.8624	0.8347
12.5	23.6.75	0.9177	-1.7532	0.9555
12.5	1.7.75	0.9029	-1.7189	1.0081
11.2	22.11.75	0.9682	-1.7988	0.9405
10.0	2.6.75	0.8978	-1.9039	0.9445
10.0	6.6.75	0.9005	-1.8355	1.0107
9.8	27.5.75	0.9478	-1.9816	0.9123
8.7	28.4.75	0.9416	-1.7783	1.0302
8.0	5.4.75	0.9324	-1.9957	0.9816

(Table 43) against the experimental temperature (T) in °C. The linear regression of these data yields the following equation:

$$a = -0.0001 + 0.0014\,T \qquad (3)$$

The slope (b) also varies with temperature, so the slope (b) for the fitted equations at the experimental temperatures (Table 43) was plotted against the experimental temperature (T) in °C. The linear regression of these data yields the following equation:

$$b = 1.0546 - 0.0083\,T \qquad (4)$$

By substituting the value for a in equation 3 for a in equation 1 and the value b in equation 4 for b in equation 1, the following relationship was derived:

$$F = (-0.0001 + 0.0014\,T)\,W^{(1.0546 - 0.0083\,T)}$$

Using this derived model the faeces production was calculated for each month (Table 44). The temperature used in the model was the average sea water temperature for that month. The slope and intercept were calculated for each temperature and a regression equation derived (Table 44). The weight of each animal in the population (Table 11) per kg dry weight of fucoid was substituted for W and the faecal production per day in grams obtained. The ingestion was calculated each month using the C/F ratio of 1:.8. The ingestion and faecal production in grams was converted to calories. The calorific value of the faeces was 1.71 ± 0.2 Kcals/g or 3.48 ± 0.41 Kcals/ash free g, as the ash content was 50.75%. The calorific value of the food, F. serratus and F. vesiculosus depended on the season (Table 45). The annual ingestion for the population per kg dry weight of fucoid was 234 Kcals and the faecal production 63.9 Kcals, which gave an assimilation efficiency of 72.7%. The assimilation efficiencies calculated by the ash-ratio method of Conover were 74.6 and 70.6 if F. serratus and F. vesiculosus respectively were the food source. If the food source was mixed (50 : 50) the assimilation efficiency would be 72.6%. The average daily ingestion index was 3.28.

The urine / faecal (U/F) production ratio was calculated at five

Table 44 *Littorina littoralis*: Parameters for the regression of log faeces production in g/day on log dry flesh weight in g. Also the ingestion and faeces production of the population per kg. dry weight of fucoid.

Month	Temperature (°C)	Intercept	Slope	Faeces (Kcals/month)	Ingestion (Kcals/month)
January	8.4	-1.9508	0.9849	4.23	14.36
February	7.5	-1.9682	0.9924	3.26	11.04
March	7.4	-1.9725	0.9932	3.60	12.18
April	8.3	-1.9337	0.9850	3.90	14.06
May	9.4	-1.8884	0.9766	4.62	16.84
June	11.9	-1.7927	0.9559	5.75	21.81
July	14.3	-1.7081	0.9360	7.22	27.39
August	15.0	-1.6947	0.9301	7.59	28.85
September	14.3	-1.7081	0.9360	6.98	26.32
October	13.0	-1.7527	0.9467	6.53	24.31
November	11.3	-1.8146	0.9609	5.43	20.87
December	10.0	-1.8643	0.9716	4.76	16.01

Table 45 *Littorina littoralis*: The calorific value of *F. serratus* and *F. vesiculosus* each month.

Month	*F. serratus*		*F. vesiculosus*	
	Kcals/g.	Kcals/ash free g.	Kcals/g.	Kcals/ash free g.
January	3.23 ±0.02	4.07 ±0.03	3.50 ±0.05	4.56 ±0.06
February	3.22 ±0.02	4.06 ±0.02	3.48 ±0.02	4.53 ±0.03
March	3.22 ±0.04	4.06 ±0.05	3.37 ±0.02	4.31 ±0.03
April	3.43 ±0.04	4.32 ±0.05	3.22 ±0.04	4.18 ±0.05
May	3.47 ±0.03	4.37 ±0.04	3.32 ±0.05	4.32 ±0.06
June	3.61 ±0.03	4.54 ±0.03	3.27 ±0.04	4.26 ±0.05
July	3.61 ±0.03	4.55 ±0.04	3.32 ±0.04	4.31 ±0.05
August	3.62 ±0.03	4.56 ±0.04	3.35 ±0.02	4.35 ±0.03
September	3.59 ±0.03	4.52 ±0.03	3.58 ±0.02	4.66 ±0.03
October	3.54 ±0.05	4.46 ±0.06	3.46 ±0.02	4.50 ±0.03
November	3.65 ±0.05	4.61 ±0.06	3.51 ±0.02	4.56 ±0.03
December	3.20 ±0.03	4.03 ±0.04	3.57 ±0.02	4.64 ±0.03

temperatures (Table 46), and this ratio (0.0046) used to calculate the annual production which was 0.29 Kcals per kg dry weight of fucoid.

Discussion

The ingestion rate and faecal production were similar whether the littorinids fed on F. serratus or F. vesiculosus. The annual measured ingestion of the animals per kg dry weight of fucoid was 234 Kcals. The annual ingestions calculated by the ash-ratio method of Conover were 251.4 and 216.8 Kcals when feeding on F. serratus and F. vesiculosus respectively. However during the year the food ingested will be a combination of the two fucoids, and if in equal proportion the ingestion would be 232.9 Kcals/ kg dry wt. fucoid which is very similar to that measured, i.e. 234 Kcals/ kg dry wt. fucoid.

The ingestion rate was temperature dependent; the ingestion each month increased with an increase in temperature or vice versa.

The assimilation efficiencies calculated by Bray (1974) of 67.8 and 74.8% for F. serratus and F. vesiculosus are very similar to those of 74.6 and 70.6% determined here.

Guiterman (1970) calculated littorinid feeding rates over a six month period (Table 47) and the results from this study over a similar period are 60% higher than those recorded by Guiterman (1970). The ingestion rate in April was similar in both studies, but Guiterman's rates for May and June were lower than for April though his rates for July and August were similar to those for April. Thus unless his April rates were an over-estimate Guiterman's rates were not temperature dependent. This is unlikely, therefore his summer rates were probably under-estimates. If his summer rates were under-estimates the true rates were probably similar to the rates measured in this study, which were temperature dependent.

The annual ammonia production of the animals per kg dry weight of fucoid was negligible (0.29 Kcals) compared to the faeces production (i.e. 0.46% of the faeces production, Table 46).

Table 46 Littorina littoralis: Ammonia and faecal production and their ratio measured in the laboratory.

Temperature (°C)	Date	Ammonia (U) (Kcals)	Faeces (F) (cals)	U/F
9.8	25.5.75	0.92	115.0	0.0080
10.0	2.6.75	0.96	323.5	0.0030
10.0	6.6.75	0.60	166.9	0.0036
14.3	19.10.75	1.55	353.3	0.0044
15.0	23.9.75	2.68	634.2	0.0042
			Average	0.0046

Table 47 Littorina littoralis: Comparison of the rate of ingestion (g. dry weight fucoid/day/100g body dry weight lirrorinid) between this study and Guiterman (1970).

Month	Ingestion	
	This study	Guiterman
March	3.50	1.90
April	3.37	3.50
May	3.87	2.40
June	4.47	2.40
July	6.03	3.60
August	6.35	3.60

4. Nucella lapillus

Introduction

Moore (1938b) records that in many localities the diet of N.lapillus consists entirely of barnacles, mainly Balanus balanoides or Chthamalus stellatus, although dog-whelks from the lower shore levels may be found in association with B. perforatus and B. crenatus. In localities where Mytilus edulis is available as an alternative source of food barnacles may be partially or completely omitted from the diet in proportion to the number of bivalves present (Moore, 1936). There are a few records of dog-whelks feeding upon bivalves other than Mytilus, Hancock (1960) mentioning small oysters and Cardium edule. Predation upon other prosobranchs has frequently been observed, Moore (1938b) recording attacks by Nucella upon P. vulgata, Gibbula cineraria, G. umbilicalis, Littorina littorea, L. littoralis and even other members of its own species.

Adult dog-whelks invariably attack other molluscs by drilling a circular hole through the shell with the radula (Pelseneer 1935, Jensen 1951 and Carricker 1955). In most cases barnacles are attacked by forcing apart the opercular plates with the proboscis. Connell (1961) demonstrated that under natural conditions Nucella shows a marked preference for the larger specimens of B. balanoides, and as it takes about the same time for a dog-whelk to open any barnacle this would be obviously advantageous.

Earlier information suggests that the diet of young dog-whelks is restricted. Colton (1916) stated that newly-hatched dog-whelks may eat small specimens of Mytilus edulis, while Moore (1938a) found that he could only rear young dog-whelks in the laboratory on a diet of Spirorbis as they would not eat barnacles. Largen (1967) demonstrated that young dog-whelks prey upon a considerable number of species of both molluscs and barnacles and that cannibalism is common, Largen (1967) and Crothers (1974) have reared Nucella to at least one year old on a diet of barnacles (Elminius).

Dog-whelks do not produce discrete faecal pellets. The waste products are released largely as ammonia.

Materials and method

The rate of feeding upon barnacles (B. balanoides) was recorded over a period of five days at the ambient temperature and cycle of tidal emersion and immersion, the dog-whelks being provided with barnacle covered rocks from which the shells of all dead barnacles had been removed. At the end of each experimental period these rocks were examined and the number and length of the barnacles which had been devoured were recorded. It was found relatively easy to determine which barnacles had been eaten by dog-whelks and which had died from other causes. After the flesh has been eaten the opercular plates either become completely detached or they fall into the empty shell, but when the barnacle dies from other causes it always does so with the cirri, and sometimes part of the body, extended from the shell. In such cases it can be clearly seen that the body is intact. The dog-whelks were collected from the study ledge.

The dry weight of the dog-whelks was determined when the experiment was terminated. Other barnacle covered rocks collected next to the ones used in the experiments were brought into the laboratory. Length and dry weight of approximately thirty of the barnacles were determined. A regression equation was determined for the barnacles of dry body weight on length. The lengths of the devoured barnacles were substituted in the regression equation and their dry weights obtained. The calorific value of the barnacle flesh was determined each month from dry weight samples of the flesh, using the Phillipson micro-bomb calorimeter.

The barnacle covered rocks were immersed for a 12-hour period prior to and after the time period (5 days) during which the dog-whelks were kept in the feeding chambers. The sea water added to immerse the feeding chambers was analysed before and after each immersion period for ammonia, following the Berthelot procedure. The rate of ammonia production by barnacles was calculated for the 12-hour period prior to and after the time period that the dog-whelks were added to the feeding chambers. The difference in ammonia concentration of the sea water before and after the immersion period enabled the ammonia production to be calculated for both dog-whelks and barnacles. As the barnacles' ammonia production rate had already been calculated the dog-whelk production rate could easily be derived. Dog-whelks were also added to feeding chambers with no barnacles. This enabled the ammonia production to be calculated for non-feeding dog-whelks.

Results

The percentage of animals feeding in the laboratory was often higher than that observed in the field, so to correct for this the number of experimental animals feeding each immersion was recorded (i.e. recorded twice in a 24-hour period). The dry weight of consumed barnacle flesh was divided by the number recorded feeding and doubled. Thus the dry weight of flesh consumed per day for a feeding dog-whelk was obtained. The linear relationship between ingestion (I) and body weight (W) in animals belonging to the same species is: $\log I = \log a + b \log W$ (see page 93). A log regression was calculated of log ingestion on log body weight for each experimental temperature (Table 48).

A model combining the temperature and size was constructed by plotting the intercept (a) for the fitted equations at the experimental temperature (Table 48) against the experimental temperature (T) in °C. The linear regression of data yields the following equation:

$$a = -0.0488 + 0.0093\,T$$

The slope (b) also varies with temperature, so the slope (b) for the fitted equations at the experimental temperatures (Table 48) was plotted against the experimental temperature (T) in °C. The linear regression of these data yields the following equation:

$$b = 0.4624 + 0.0069\,T$$

By substituting the values for a and b in the equation $I = aW^b$, the following relationship was derived:

$$I = (-0.0488 + 0.0093\,T)\,W^{(0.4624 + 0.0069\,T)}$$

For each month the average sea water temperature (in ^{o}C) was substituted for T so enabling the intercept (a) and slope (b) to be calculated for the regression equations of log ingestion on log flesh weight (Table 49). Each month all the dog-whelks in the study area were measured and their corresponding flesh weight calculated from regression equations (Table 14). The dry flesh weight of the dog-whelks in the study area were substituted and the dry body weight of barnacles ingested calculated. The regression equations were for animals feeding continuously. The percentage of dog-whelks feeding in the study area was observed on a number of occasions each month, from which the average percentage of dog-whelks feeding per day for each month was calculated (Table 50). The ingestion calculated from the regression equations was multiplied by the proportion feeding (Table 49). The dry body weight of the ingested barnacles was converted to calories (Table 51). The annual juvenile and adult ingestions were 265 Kcals and 120 Kcals (Table 49) respectively, giving a total for the population of the study area of 385 Kcals. The average daily ingestion index for the study area population was 1.53.

The rate of ammonia production was calculated for the feeding and non-feeding dog-whelks at the experimental temperatures. Regression equations were calculated of log ammonia production on log flesh weight for the feeding and non-feeding dog-whelks for each experimental temperature (Tables 52 & 54).

Two models were calculated combining temperature and size (see page 96). The values of intercept (a) and slope (b) were obtained from tables 52 and 54. The models determined are :

for feeding animals: $U = (-4.1301 + 1.0092\,T)\,W^{(0.5949 + 0.0012\,T)}$

for non-feeding animals: $U = (-1.4206 + 0.3415\,T)\,W^{(0.7391 - 0.0043\,T)}$

For each month the average sea water temperature (in^{o}C) was substituted for T, which allowed the intercept (a) and slope (b) to be

Table 48 *Nucella lapillus*: Parameters for the regression of log consumption in cals/day on dry body weight in g.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.0	23.9.75	0.8872	-0.9554	0.6803
14.5	26.7.75	0.8710	-0.9915	0.7009
14.3	19.10.75	0.9427	-1.2027	0.4336
12.5	23.10.75	0.9129	-1.2365	0.5057
11.6	20.6.75	0.9638	-1.3879	0.3689
10.0	2.6.75	0.8714	-1.6706	0.2801
10.0	6.6.75	0.9006	-1.3847	0.5360
9.8	25.5.75	0.9285	-1.1356	0.7815
8.7	30.4.75	0.8970	-1.4731	0.5490
7.4	19.3.75	0.9431	-1.5705	0.5731

Table 49 *Nucella lapillus*: Parameters for the regression of log consumption in cals/day on dry body weight in g. and the juvenile and adult consumption each month.

Month	Temperature (°C)	Intercept	Slope	Consumption juvenile (Kcals)	adult (Kcals)	total (Kcals)
January	8.4	-1.5291	0.5203	5.98		5.98
February	7.5	-1.6054	0.5141	1.73		1.73
March	7.4	-1.6159	0.5134	7.15	3.87	11.02
April	8.2	-1.5283	0.5196	10.02	7.30	17.32
May	9.4	-1.4308	0.5272	15.91	10.88	26.78
June	11.9	-1.2392	0.5445	21.65	17.14	38.79
July	14.3	-1.0744	0.5610	45.26	20.75	66.01
August	15.0	-1.0422	0.5659	52.95	5.83	58.78
September	14.3	-1.0744	0.5610	50.76	21.13	71.89
October	13.0	-1.1650	0.5521	26.65	19.32	45.96
November	11.28	-1.2631	0.5402	17.56	14.19	31.74
December	10.0	-1.3511	0.5314	9.31		9.31

Table 50 Nucella lapillus: The percentage of individuals observed feeding in the course of a single low tide.

Month	Percentage feeding Mature	 2nd & 3rd year juveniles	 1st year juveniles
January	0	32	44
February	0	14	17
March	38	65	76
April	66	67	71
May	77	80	90
June	79	83	98
July	65	91	100
August	18	92	93
September	75	92	93
October	62	62	52
November	60	28	30
December	0	44	47

Table 51 Balanus balanoides: Calorific value of the body.

Month	Kcals/g.		Kcals/ash free g.	
January	4.19	±0.07	5.13	±0.09
February	4.12	±0.03	5.05	±0.04
March	4.07	±0.02	4.99	±0.02
April	4.21	±0.04	5.16	±0.05
May	4.40	±0.05	5.39	±0.06
June	4.61	±0.04	5.65	±0.05
July	4.67	±0.04	5.72	±0.05
August	4.67	±0.04	5.72	±0.05
September	4.67	±0.04	5.72	±0.05
October	4.67	±0.05	5.72	±0.06
November	4.56	±0.03	5.59	±0.04
December	4.21	±0.03	5.16	±0.04

Table 52 *Nucella lapillus*: Parameters for the regression of log egestion (ammonia production in g/day) on dry body weight in g. for feeding animals.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.0	23.9.75	0.9374	1.0264	0.5902
14.5	26.7.75	0.9465	1.0165	0.5867
14.3	19.20.75	0.9379	1.0553	0.6454
12.5	23.10.75	0.9681	0.9175	0.6342
11.6	20.6.75	0.9702	0.8614	0.6061
10.0	2.6.75	0.9647	0.8283	0.6730
10.0	6.6.75	0.9500	0.6537	0.5364
9.8	25.5.75	0.9826	0.8348	0.7045
8.7	30.4.75	0.9734	0.4970	0.4717
7.4	19.3.75	0.9682	0.5753	0.6458

Table 53 *Nucella lapillus*: Parameters for the regression of log egestion (ammonia production in g/day) on dry body weight in g. and the egestion each month of feeding animals.

Month	Temperature (°C)	Intercept	Slope	Egestion juvenile (Kcals)	Egestion adult (Kcals)	Egestion total (Kcals)
January	8.4	0.6340	0.6049	1.02		1.02
February	7.5	0.5372	0.6039	0.30		0.30
March	7.4	0.5283	0.6037	1.24	0.75	2.00
April	8.3	0.6288	0.6048	1.70	1.37	3.07
May	9.4	0.7280	0.6061	2.62	1.94	4.57
June	11.9	0.8967	0.6091	3.44	2.95	6.38
July	14.3	1.0122	0.6120	7.28	3.53	10.81
August	15.0	1.0471	0.6129	8.49	0.09	8.58
September	14.3	1.0122	0.6120	8.20	3.60	11.79
October	13.0	0.9545	0.6105	4.22	3.30	7.52
November	11.3	0.8677	0.6084	2.85	2.26	5.11
December	10.0	0.7675	0.6069	1.63		1.61

Table 54 Nucella lapillus: Parameters for the regression of log egestion (ammonia production in g/day) on dry body weight in g. for non-feeding animals.

Temperature (°C)	Date	Correlation coefficient	Intercept	Slope
15.0	23.9.75	0.9241	0.6080	0.7317
14.5	26.7.75	0.9237	0.4073	0.5324
14.3	19.10,75	0.9468	0.6583	0.8113
12.5	23.10.75	0.9872	0.2567	0.5183
11.6	20.6.75	0.9889	0.4631	0.7880
10.0	2.6.75	0.9710	0.1873	0.5811
10.0	6.6.75	0.9655	0.4666	0.9054
9.8	25.5.75	0.9423	0.2047	0.6239
8.7	30.4.75	0.9654	0.2058	0.7096
7.4	19.3.75	0.9721	0.0465	0.6944

Table 55 Nucella lapillus: Parameters for the regression of log egestion (ammonia production in g/day) on dry body weight in g. and the egestion each month of non-feeding animals.

Month	Temperature (°C)	Intercept	Slope	Egestion juvenile (Kcals)	 adult (Kcals)	 total (Kcals)
January	8.4	0.1609	0.7029	0.39	0.84	1.23
February	7.5	0.0571	0.7068	0.41	0.57	0.98
March	7.4	0.0439	0.7072	0.16	0.36	0.53
April	8.3	0.1504	0.7034	0.13	0.21	0.34
May	9.4	0.2527	0.6986	0.10	0.17	0.27
June	11.9	0.4221	0.6879	0.32	0.23	0.56
July	14.3	0.5394	0.6776	0.06	0.56	0.62
August	15.0	0.5684	0.6746	0.21	1.33	1.54
September	14.3	0.5394	0.6776	0.21	0.35	0.56
October	13.0	0.4798	0.6832	0.55	0.57	1.13
November	11.3	0.3870	0.6905	0.19	0.44	0.63
December	10.0	0.2998	0.6961	0.45	1.24	1.69

calculated for the regression equations of log ammonia production on log weight (Tables 53 & 55). The lengths of the dog-whelks in the study area were substituted and the ammonia production calculated. The ammonia production was converted to calories using the Brafield and Solom$\overset{o}{a}$n (1972) ? coefficient of 68.9 Kcals/mol. The annual egestion (i.e. ammonia production) for the feeding and non-feeding animals was 63 and 10 Kcals respectively, giving a total of 73 Kcals for the study population.

Discussion

No adults were observed feeding from the end of November to early March, and only a few in March, late July and August. During the rest of the year 60 - 75% of the adults were feeding at any one time. During the periods when none or few adults were feeding they were in aggregations in crevices and rock pools. These aggregations were connected with breeding (see page 75).

Eighty to one hundred percent of the juveniles were feeding at any one time in the spring and summer. The percentage decreased as the autumn and winter progressed reaching a minimum of 15% in February 1975. Connell (1961) noticed also that at any one time not all the dog-whelks were feeding. He also noticed that in the winter only a low percentage of juveniles were feeding at any one time. Low winter temperatures can prevent feeding (Largen 1967, Feare 1970 & 1971). Largen (1967) determined that below 3°C dog-whelks became completely inactive, but above 3°C both activity and rate of feeding increased rapidly reaching a maximum a little above 20°C. The minimum sea temperature recorded for Derbyhaven between 1973 and 1976 was 7.1°C. Thus the winter sea temperature was not low enough to inhibit feeding. The rough weather also affected feeding, and if the sea was rough fewer animals than normal were feeding and the animals tended to aggregate in crevices and rock pools. In the winter a greater percentage of the juveniles were feeding at any one time in the laboratory feeding experiments maintained at the ambient field sea temperature than on the shore. The sea was rough for the greater part of the winter so it is likely that the roughness of the sea rather than low temperature inhibits feeding. When the sea was rough the animals tended to aggregate in crevices and rock pools. This was probably a defence mechanism to reduce the chances of dislodgement, for if the animals were dislodged they would be likely to be washed away to possibly an unfavourable area of the shore.

On many shores in Britain the juveniles do not feed during the winter (Cowell and Crothers 1970, Feare 1970, Crothers 1971 & 1974). At Derbyhaven during the winter only a low percentage of juveniles were observed feeding at any one time, so this did not reveal whether all of the juveniles feed during the winter. By examining the adult shell one can determine whether they feed during the winter when juvenile. A row of 'teeth' are laid down on the inner margin of the shell at maturity (see page 39). Any more than one row of 'teeth' indicates prolonged interruptions of growth when juvenile i.e. periods of non-feeding. Very few adults on the Derbyhaven shore had more than one row of 'teeth' so all the juveniles at Derbyhaven obviously feed throughout the winter. Cowell and Crothers (1970) determined that the frequency of multiple rows of 'teeth' was high on exposed shores, and also Feare (1970) on the Yorkshire coast where the winter sea temperature was low.

Previous workers (Connell 1961, Largen 1967) have measured feeding rates but only as the number of barnacles consumed per dog-whelk, giving no indication of the weight of the dog-whelks or weight of the barnacle flesh concerned. However if the feeding rates are compared (Tables 56, 57 & 58), it is apparent that the rate of barnacles consumed increases with increasing temperature. Connell (1961) determined his feeding rates at Millport, therefore the seasonal sea temperature is likely to be very similar to that at Derbyhaven, and as can be expected Connell's seasonal feeding rates are very similar to those of this study. Also Largen's (1967) feeding rates at various temperatures correspond closely to this study's

Table 56 Nucella lapillus: Feeding rates (number of Balanus balanoides eaten per day per animal) measured in the laboratory.

Temperature (°C)	Juveniles Length 1.6 - 2.0 cm	Juveniles Length 2.0 - 2.6 cm	Adults Length 2.4 - 2.8 cm
15.0	0.88	1.67	2.67
14.5	0.58	1.27	2.09
14.3	0.80	1.56	1.46
12.5	0.76	0.66	1.00
11.6	0.92	0.69	0.69
10.0	0.12	0.79	
10.0	0.52	0.70	
9.8	0.56	0.50	
8.7	0.40	0.36	
7.4	0.32	0.37	

Table 57 Nucella lapillus: The feeding rates (number of Balanus balanoides eaten/day/animal) determined by Connell (1961). The lengths of the dog-whelks were between 2.0 and 2.6 cm.

Season	Winter	Spring	Summer	Autumn
Feeding rates	0.21	0.44	2.38	0.85

Table 58 Nucella lapillus: The influence of water temperature upon the rate of feeding (number of barnacles eaten per day per animal) recorded by Largen (1967).

Temperature (°C)	3	5	10	15	20
Feeding rates	0.06	0.14	0.80	1.49	2.29

feeding rates determined for the juveniles, length 2.0 - 2.6 cm.

During the winter the adults were collected from aggregations in crevices and placed in feeding chambers with barnacles at the ambient field sea water temperature, but very few of the animals made any attempt to feed and therefore no feeding rates were determined for the winter temperature (see Table 56). The dog-whelks tend to feed on the larger barnacles present in the feeding chambers. Therefore, as can be expected, the feeding rates of the larger dog-whelks were higher.

Faecal production was not measured. However the faecal production was probably low compared to ammonia production and is discussed later (see page 121).

CHAPTER 6

THE ENERGY BUDGETS

The energy budget of a population may be summarized by the equation

$$C = P + R + F + U \qquad \text{where} \quad P = Pr + Pg$$

Each component was measured in kilocalories per annum. C, energy content of the food consumed; P, total energy converted to flesh (Pg) and gametes (Pr); R, energy lost due to metabolism; F, energy lost due to faeces; U, energy lost due to urine and other exudates; C - F - U is the proportion of ingested energy which is assimilated (A) by the population.

In order to obtain maximum information on rates and efficiencies in the energy equation it is desirable to study populations in a steady-state condition. 'We restrict attention to steady states since seasonal differences in climate and physiology, combined with essentially random meteorological or biological events in short term data collections, will permit so much variance as to obscure real consistencies and differences.' (Slobodkin 1962). The <u>P. vulgata</u> population was remarkably stable over the two year study period, and there were only slight increases in biomass of 1.3% and 0.25% in 1974 and 1975 respectively (Table 7). The littorinid and dog-whelk populations were observed over an eighteen month period and all the observations indicated a steady-state situation.

All the parameters of the energy budget have been measured and are:

<u>P. vulgata</u> measured in Kcals/m^2/year

In 1974 the average biomass was 80.94 Kcals/m^2.

$$\left.\begin{array}{ll} \left.\begin{array}{ll} \left.\begin{array}{ll} Pg & 13.86 \\ Pr & 22.72 \end{array}\right\} P = 36.58 \\ R & 115.66 \end{array}\right\} A = 152.24 \\ F & 410.64 \\ U & 0.42 \end{array}\right\} {}^{*}C = 563.29$$

$$\begin{array}{lll} {}^{*}C_1 & 570.6 & \text{(June)} \\ & 512.2 & \text{(August)} \\ & 468.0 & \text{(September)} \end{array}$$

In 1975 the average biomass was 84.24 Kcals/m^2.

Pg	18.88	P = 41.78	A = 163.78	*C = 606.02
Pr	22.90			
R	122.00			
F	441.70			
U	0.45			
*C_1	602.0	(June)		
	540.4	(August)		
	493.6	(September)		

<u>L. littoralis</u> measured in Kcals/Kg dry fucoid/yr

The average biomass was 23.97 Kcals/Kg dry fucoid.

Pg	35.38	P = 55.27	A = 171.80	*C = 235.95
Pr	19.89			
R	116.53			
F	63.86			
U	0.29			
*C_1	234.04			
	232.90			

<u>N. lapillus</u> measured in Kcals/m^2/year.

The average biomass was 5.74 Kcals/m^2.

Pg	5.26	P = 5.94	A = 24.11	*C = 29.34
Pr	0.68			
R	18.17			
F				
U	5.23			
*C_1	32.11			

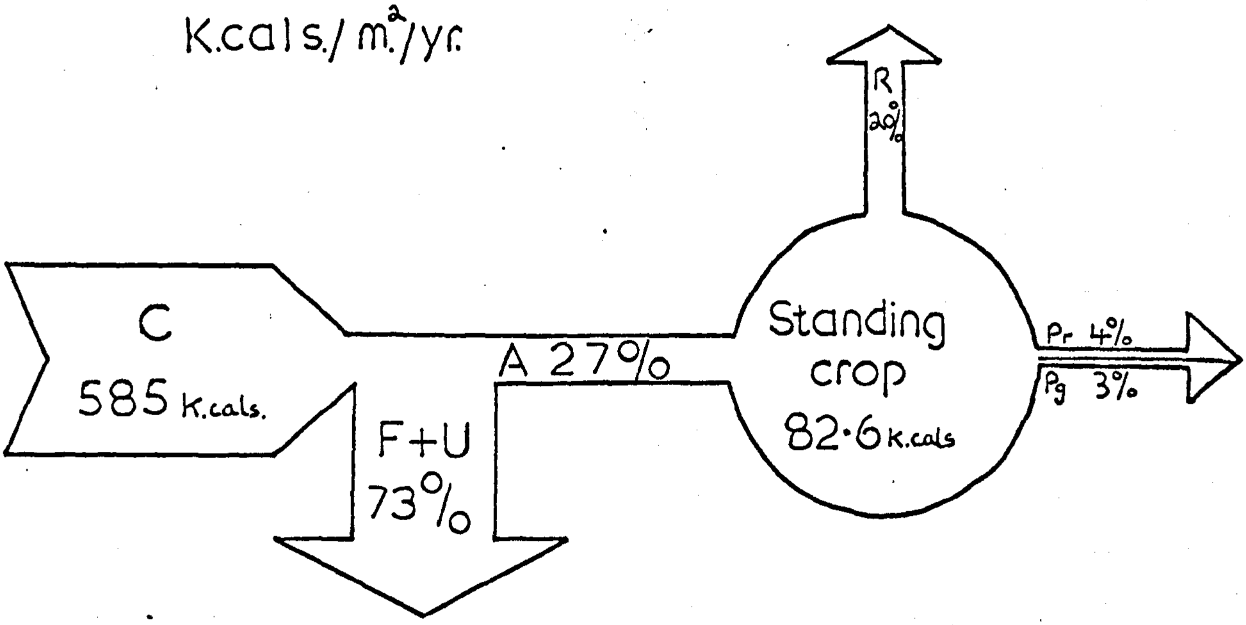
*C This value of ingestion was calculated by summing the components of the budget equation (A + F + U)

C_1 This value of ingestion was determined by direct measurement.

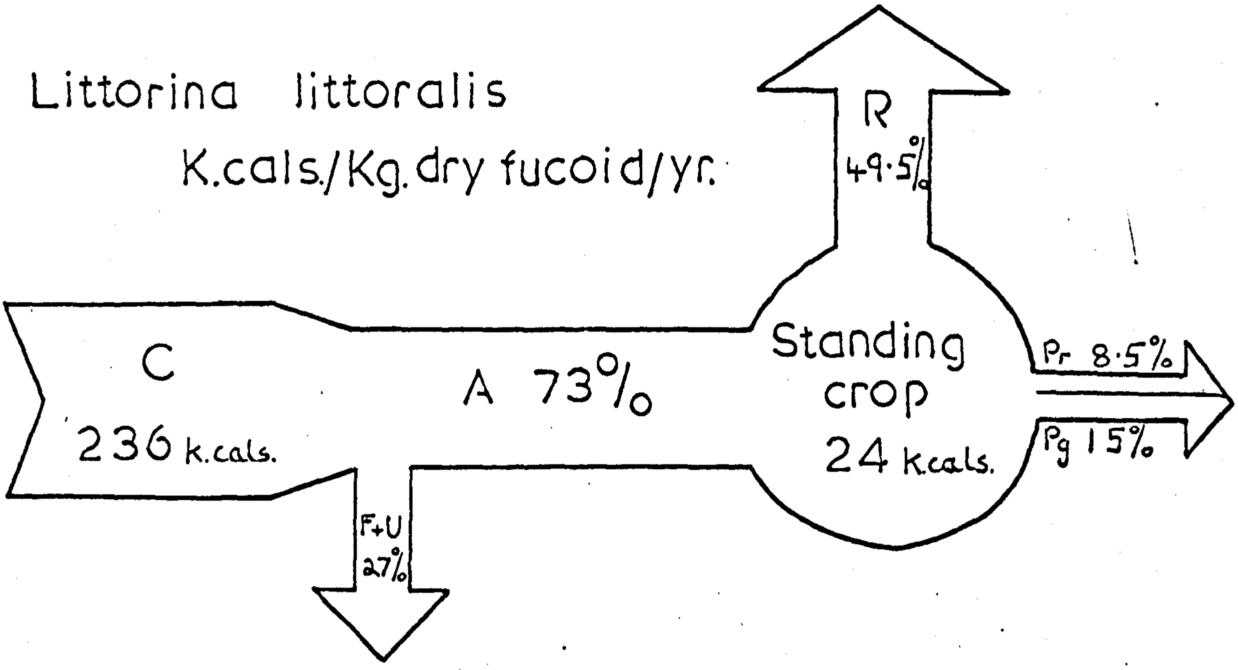
This study, unlike the majority, provided an internal check on the energy budget equation. <u>P. vulgata</u>'s annual energy consumption (C) calculated as A + F tallied very closely with the yearly consumption C_1) computed from the June feeding experiments (Table 39). The yearly

Fig. 21. The partitioning of the energy ingested by the three populations, P. vulgata, L. littoralis & N. lapillus.

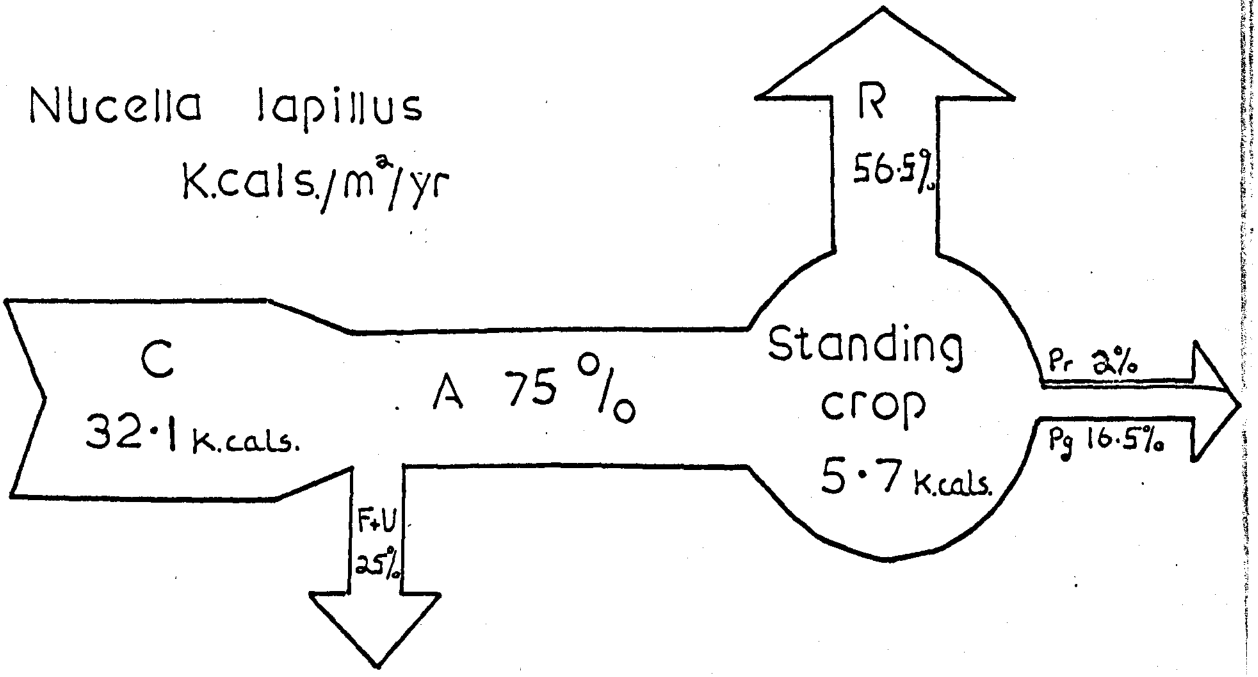
Patella vulgata
K.cals./m.²/yr.



Littorina littoralis
K.cals./Kg. dry fucoid/yr.



Nucella lapillus
K.cals./m²/yr



consumption calculated from the August and September experiments were lower possibly because the feeding rates are reduced during the period of gonadal development. The calculated yearly consumption (C) of the littorinid population checked remarkably closely with the directly measured consumption (C_1). However the consumption check for N. lapillus was not so close; the measured consumption (C_1) was 9.4% higher than that calculated (C). The egestion was undoubtedly under-estimated as there was no estimate of faecal production. However, unlike the limpets and littorinids, faecal production was probably low as the ammonia production was very high. If the measured consumption (C_1) and ammonia production were accurate then the faecal production will have been 2.76 Kcals/m^2/year.

Components of the energy budget are discussed and compared with those of marine molluscan values found in the literature (Table 59).

A high percentage of the assimilated energy (A) was lost via metabolism ($R \times 100/A$) in all three species, 75% in P. vulgata and N. lapillus and 60% in L. littoralis. These figures are within the 58 to 91% range for metabolic loss quoted in the marine molluscan literature (Table 59). Most are between 70 and 88%, so L. littoralis has a relatively low loss. MacNeil and Lawton (1970) suggested that long-lived poikilotherms, where a population is in excess of two years old, lose more of the assimilated energy via heat loss. Such animals are supposed to experience high respiratory cost non-productive periods, such as during winter at higher latitudes or during aestivation, so that annual production efficiencies are low. All three species fall into this category, though L. littoralis lives on average under three years. The littorinid's only low productivity period was when growth decreased during winter, for although growth terminated on maturity the animals spawned at regular intervals until death. N. lapillus and P. vulgata both had non-productive periods since the former stopped growing on maturity and was then non-productive except for two periods each year when spawning took place. Although growth in the latter

Table 59 A comparison of various energy budget components for various marine molluscs.

Species	Units	A	P	$\frac{R \times 100}{A}$	$\frac{A \times 100}{C}$	$\frac{P \times 100}{A}$	$\frac{E \times 100}{C}$	$\frac{P}{B}$	$\frac{A \times 100}{P}$	$\frac{P \times 100}{C}$	I index	Source
Aplysia punctata	Kcals/80 days			59-82	59-71	18-41			32-53	15-35		Carefoot (1967)
Modiolus demissus	Kcals/m^2/yr	56	16.7	70		30		0.28	17			Kuenzler (1961)
Mytilus edulis	g/78 days		29.7					0.36		10.0		Tenore et al.(1973)
Crassostrea virginica	g/78 days		51.0					0.46		18.4		Tenore et al.(1973)
Crassostrea virginica	Kcals/m^2/yr	9780	4132	58		42		2.01	16			Dame (1976)
Mercenaria mercenaria	g/78 days		54.1					0.45		23.7		Tenore et al. (1973)
Scrobicularia plana	Kcals/m^2/yr	336	70.8	79	61	21	2.4	0.59	48	12.8	1.26	Hughes (1970)
Tellina tenuis	mg/yr	38	8	79		21		0.40	45			Trevallion (1971)
Nerita tessellata	Kcals/m^2/yr	244	29.3	88	40	12	3	0.78	29	4.8	4.45	Hughes (1971 b)
Nerita versicolor	Kcals/m^2/yr	58.5	7.6	87	39	13	5	0.63	12	5.1	4.00	Hughes (1971 b)
Nerita pelomata	Kcals/m^2/yr	154	21.7	86	43	14	5	1.25	17	6.1	5.64	Hughes (1971 b)

(continued)

Table 59 (continued)

Species	Units	A	P	$\frac{Rx100}{A}$	$\frac{Ax100}{C}$	$\frac{Px100}{A}$	$\frac{Ex100}{C}$	$\frac{P}{B}$	$\frac{Ax100}{P}$	$\frac{Px100}{C}$	I index	Source
Fissurella barbadensis	Kcals/m^2/yr	190	50.8	73.3	34	27	8.0	4.10	10	9.2	12.21	Hughes (1971a)
Tegula funebralis	Kcals/m^2/yr	637	59	91	59	9	4	0.47	15	5.5	2.36	Paine (1971)
Littorina irrorata	Kcals/m^2/yr	290	40.6	86	45	14		0.81		6.3	3.5	Odum & Smalley (1959)
Littorina littorea	Kcals				87						1.27	Grahame (1973)
S. Floridian Littorinidae	g/m^2/yr		12.1					1.27 to 5.54	65 to 85			Borkowski (1974)
Patella vulgata (1974)	Kcals/m^2/yr	152	36.6	76	27.0	24	2.3	0.45	62	6.6	2.07	This study
Patella vulgata (1975)	Kcals/m^2/yr	164	41.8	74	27.0	26	3.2	0.50	55	7.1	2.13	This study
Littorina littoralis	Kcals/m^2/yr	138	55.3	60	72.7	40	17.0	2.30	36	23.4	2.31	This study
Nucella lapillus	Kcals/m^2/yr	24.1	5.9	75	75.1	25	16.4	1.04	11.4	18.5	1.53	This study

continued throughout life, it was practically negligible in the animals over four years. Gonad development and spawning take place in late summer to early winter, so therefore these animals were relatively non-productive from mid-winter to early summer.

The net growth efficiency (P x 100/A) is the percentage of assimilated energy not lost via metabolism, which was 25% for P. vulgata and N. lapillus and 40% for L. littoralis. These are within the range, 9 to 42%, quoted in the marine molluscan literature (Table 59).

The assimilation efficiencies (A x 100/C) were 27, 73 and 75% for P. vulgata, L. littoralis and N. lapillus respectively. The range in the marine molluscan literature is 34 to 87%, and the limpet's efficiency was below this range. P. vulgata ingests numerous species of sporelings, algae, diatoms, etc. and probably lacks the necessary enzymes to digest many of them, which would account for the low assimilation efficiency. Fissurella barbadensis (Keyhole limpet) has a similar feeding behaviour to P. vulgata and also has a low efficiency of 34%, (Hughes 1970). According to Ward (1967) all the ingested material except the blue-green algae passes through the gut relatively unchanged. The assimilation efficiencies for Aplysia punctata varied between 59.71% depending on the food species Carefoot 1966). The littorinids and dog-whelks have high efficiencies compared with most molluscan species (Table 59). Welch (1968) states that the lower the assimilation efficiency of an animal the higher is its net growth efficiency, or in simple terms, the less energy an animal extracts from its food the greater is the percentage used for growth, and the smaller is that used for respiration. The net growth efficiency was plotted against assimilation efficiency using data from this study and the marine molluscan literature (Fig. 22). The points, for all but L. littoralis, do not fall near Welch's plotted line and certainly do not show his relationship. The line Welch determined was computed using a variety of marine and fresh water animals which included only one molluscan species, Aplysia punctata.

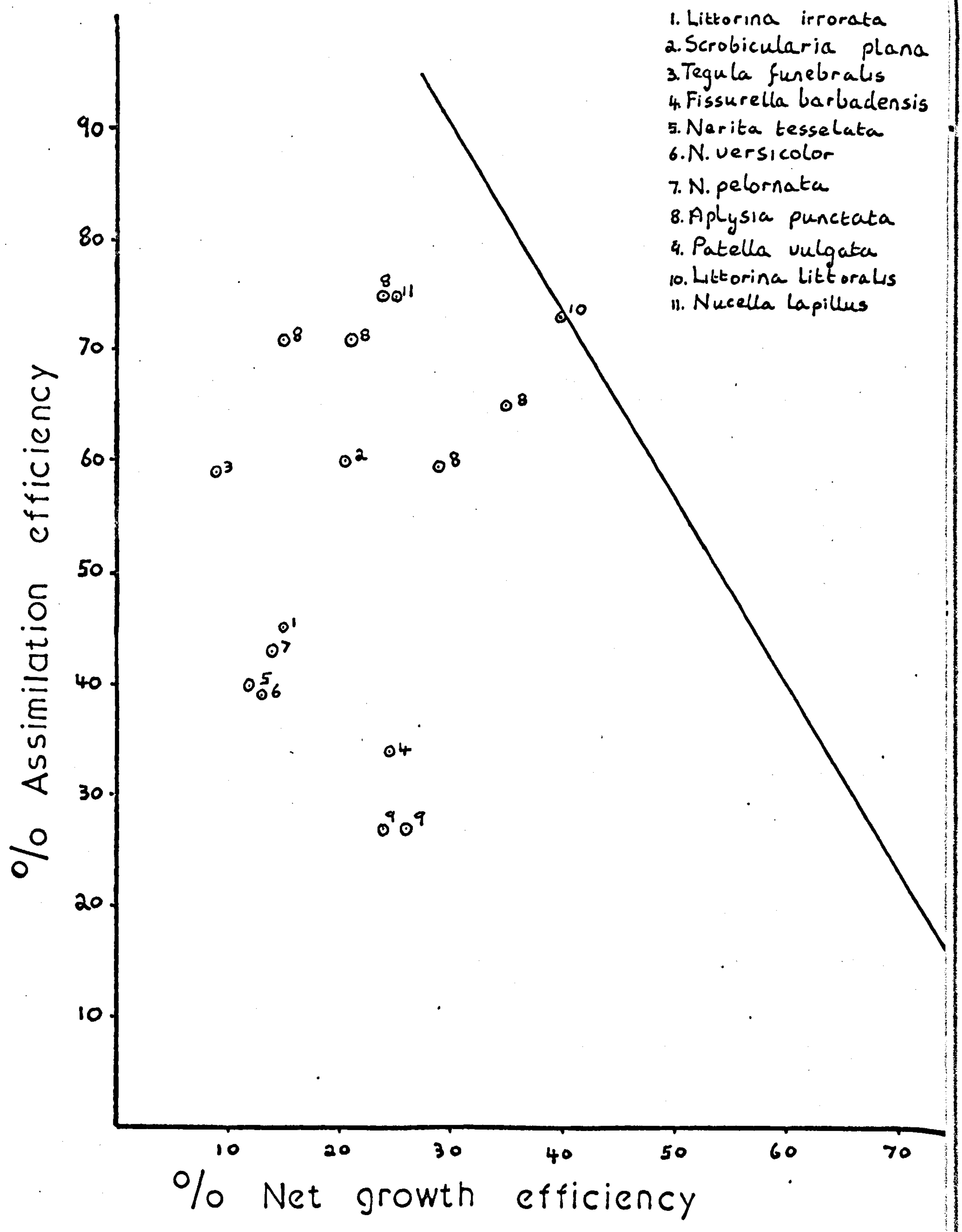


Fig. 22. Net growth efficiency plotted against assimilation efficiency for some marine molluscan consumers (o) and Welch's (1968) plot (—).

Marine molluscs appear to have no relationship at all between assimilation efficiency and net growth efficiency, which is contrary to Welch's statement.

The ecological efficiencies (E x 100/C, where E is mortality) were 2.3 to 3.2, 17 and 16.4% for P. vulgata, L. littoralis and N. lapillus respectively. P. vulgata had a low efficiency as the population was dominated by older animals (6 - 8 years) which have a low annual mortality. Although the juvenile mortality was high it was more or less negligible compared to the biomass of the population. L. littoralis and N. lapillus had a very high efficiency. Their mortality rates were very high, for adults as well as juveniles. P. vulgata, especially the adults, probably had very few predators on this shore, whereas a large number of species of fish, birds and crustaceans feed on littorinids and dog-whelks (see Pettitt, 1975).

The turn-over rates (P/B, where B is the average biomass) for P. vulgata, L. littoralis and N. lapillus were 0.45 to 0.50, 2.30 and 1.04 respectively. The range in the marine molluscan literature was 0.28 to 5.54, with the majority under 1.0 (Table 59). P. vulgata had a low ratio due to the limpets in this population having a relatively long life expectancy (up to 13 - 15 years, Fig. 12) and being dominated by older animals (6 - 8 year olds, Table 8) which only had a low growth, so that even though the juveniles' growth production was high it had little effect on the ratio. L. littoralis had a high ratio due to the littorinids having a short life expectancy (under 3 years) with the average adult life expectancy 10 months, so the high juvenile growth production made a large contribution to the ratio. Although the adults made no growth production contribution, the spawn production was high. The life expectancy of N. lapillus was intermediate (5 to 7 years, Fig. 17), juvenile growth was very high, but the adults made no growth contribution and the spawn production was low, so the ratio was in between that of P. vulgata and L. littoralis. Using the P/B ratio it should be possible in future years to estimate the production of these three populations by measuring the mean annual biomass and multiplying this by the P/B ratio, thus avoiding the more lengthy studies required to calculate production directly. Unfortunately the P/B ratios are very limiting as they can only be safely applied to populations under the same conditions.

The relationship between annual production and annual respiration in Kilocalories/m^2/year was examined for this study and that of the literature on other marine molluscs (Fig. 23). The productions were between 1 and 100 Kcals, except for Crassostrea virginica (Dame 1976) with 4,132 Kcals; if this value is omitted model A is obtained (Fig. 23):

$$\text{where} \quad \log_{10} P = -0.0478 + 0.7253 \log_{10} R$$
$$\log_{10} R = 0.6525 + 0.9651 \log_{10} P$$

MacNeil and Lawton (1970), who examined this relationship for a large number of aquatic and marine poikilotherms, obtained a model (model B in Fig. 23) very similar to model A. Their production values were also in between 1 and 100 Kcals:

$$\text{where} \quad \log_{10} P = -0.2367 + 0.8233 \log_{10} R$$
$$\log_{10} R = 0.3757 + 1.0733 \log_{10} P$$

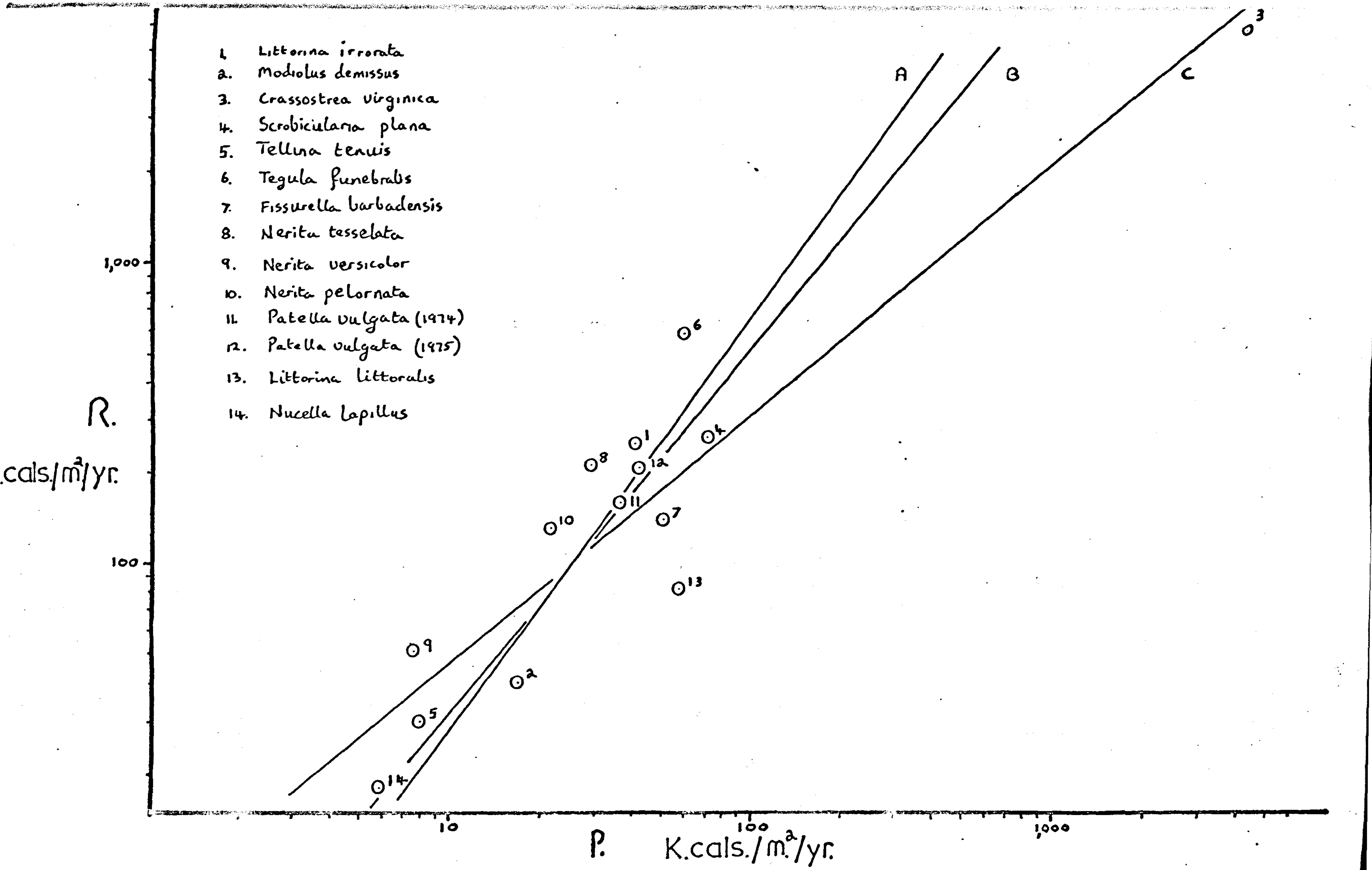
If the Crassostrea virginica value is included, model C is obtained (in Fig. 23):

$$\text{where} \quad \log_{10} P = -0.6382 + 1.0310 \log_{10} R$$
$$\log_{10} R = 0.8296 + 0.8350 \log_{10} P$$

Model A and that of MacNeil and Lawton (1970) are useful to predict year productions between 1 and 100 Kcals/m^2/year for poikilotherms but are probably not accurate if extrapolated beyond these values. Production values over 100 Kcals/m^2/year possibly require a different model, but unfortunately the data are not available to construct one.

The spawn production of P. vulgata, L. littoralis and N. lapillus comprised 62 to 55, 36 and 11.4% respectively of the combined total of somatic and spawn production (Pr x 100/P). The range in the literature for marine molluscs was 10 to 85%. This was of particular interest as until

Fig. 23. The relationship between annual production (P) and the annual respiration (R.) in marine mollusc populations. A; is the line through the points neglecting point 3. B; is Mc.Neil & Lawton's line and C; is the line through all the points.


1. Littorina irrorata
2. Modiolus demissus
3. Crassostrea virginica
4. Scrobicularia plana
5. Tellina tenuis
6. Tegula funebralis
7. Fissurella barbadensis
8. Nerita tesselata
9. Nerita versicolor
10. Nerita pelornata
11. Patella vulgata (1974)
12. Patella vulgata (1975)
13. Littorina littoralis
14. Nucella lapillus
A
B
C
R.
.cals./m²/yr.
1,000
100
10
100
1,000
P.
K.cals./m²/yr.

recently spawn production has generally been considered a relatively minor component of production, but this is obviously not the case for many marine molluscs. Limpets over four years old partition over 90% of their production into spawn, and an average seventh year limpet produced 1.09 and 1.27 Kcals of spawn respectively for males and females, while the growth production was 0.11 Kcals, so 91 and 92% of production was as spawn. All the production of the littorinids and dog-whelks was channelled into growth in the juveniles and spawn in the adults.

The growth production was partitioned as tissue and shell growth. Shell production constituted 11 to 12, 19 and 12% of the total for *P. vulgata*, *L. littoralis* and *N. lapillus*. 13% of the shell production of the dog-whelk population was partitioned for shell thickening at maturity; 18 - 21% of the shell production of individuals matured.

The gross ecological efficiency ($P \times 100/C$) for *P. vulgata*, *L. littoralis* and *N. lapillus* was 6.6 to 7.1, 23.4 and 18.5% respectively. The range in the marine molluscan literature was 5.1 to 35% (Table 59). The efficiency for *P. vulgata* was low compared to the other two (approximately a third of *N. lapillus*), largely as the assimilation efficiency was 27% compared to 72 and 75%. This meant that the limpet had to consume three times the amount of food to assimilate the same energy. The littorinid efficiency was 40% higher than the dog-whelk as the metabolic energy loss was 60% compared to 75% in the dog-whelk.

The ingestion indexes were 2.07 to 2.13, 2.31 and 1.53 for *P. vulgata*, *L. littoralis* and *N. lapillus* respectively, which fall within the range of 1.26 to 12.21 in the marine molluscan literature (Table 59).

REFERENCES

Anraku, M. 1964. Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. *Limnol. Oceanogr.*, *9* 195-206.

Bakker, K. 1959. Feeding habits and zonation in some intertidal snails. *Arch. néerl. Zool.*, *13* 230-257.

Ballantine, W.J. 1961a. A biologically defined exposure scale for the comparative description of rocky shores. *Fld. stud.*, *1* 1-19.

Ballantine, W.J. 1961b. The population dynamics of *Patella vulgata* and other limpets. Ph.D. thesis, Queen Mary College, London University, p.236.

Barkmann, J. 1955. Distribution and ecology of *Littorina obtusata*. *Arch. néerl. Zool.*, I, *11* 22-86.

Barry, R.J.C. and Munday, K.A. 1959. Carbohydrate levels in *Patella*. *J. mar. biol. Ass. U.K.*, *38* 81-95.

Blackmore, D.T. 1969a. Studies of *Patella vulgata* L. I. Growth, reproduction and zonal distribution. *J. exp. mar. Biol. Ecol.*, *3* 200-213.

Blackmore, D.T. 1969b. Studies of *Patella vulgata* L. II. Seasonal variation in biochemical composition. *J. exp. mar. Biol. Ecol.*, *3* 231-245.

Borkowski, T.V. 1974. Growth, mortality and productivity of South Floridian *Littorinidae* (Gastropoda: Prosobranchia). *Bull. mar. Sci.*, *24* 409-438.

Brafield, A.E. and Soloman, D.J. 1972. Oxycalorific coefficients for animals respiring nitrogenous substrates. *Comp. Biochem. Physiol.*, 43A 837-841.

Bray, C.J. 1974. A study of the mobility of *Littorina obtusata*. M.Sc. in Ecology, University of Wales.

Brody, S., Procter, R.C. and Ashworth, U.S. 1934. Growth and development. 34. Basal metabolism, endogenous nitrogen, creatinine and neutral sulphur excretions as functions of body weight. *Bull. Mo. agric. Exp. Stn.*, *220* 1-40.

Bryan, G.W. 1969. The effects of oil-spill removers ('detergents') on the gastropod *Nucella lapillus* on a rocky shore and in the laboratory. *J. mar. biol. Ass. U.K.*, *49* 1067-1092.

Carefoot, T.H. 1967. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. *J. mar. biol. Ass. U.K.*, *47* 565-89.

Carricker, M.R. 1955. Critical review of the biology and control of oyster drills *Urosalpinx* and *Eupleura*. *Spec. Scient. Rep. U.S. Fish. Wildl. Serv.*, *148* 1-150.

Choquet, M. 1968. Croissance et longévité de *Patella vulgata* L. (Gastéropoda: Prosobranche) dans le Boulonnais. *Cah. Biol. mar.*, *9* 449-468.

Colton, H.S. 1916. On some varieties of *Thais lapillus* in the Mount Desert region, a study of individual ecology. *Proc. nat. Acad. Sci. Philad.*, *68* 440-451.

Connell, J.H. 1961. The effects of competition, predation by *Thais lapillus*, and other factors on natural population of the barnacle *Balanus balanoides*. *Ecol. Mon.*, *31* 61-104.

Conover, R.J. 1966. Assimilation of organic matter by zooplankton. *Limnol. Oceanog.*, *11* 338-345.

Cook, A., Bamford, O.S., Freeman, J.D.B. and Tiedman, D.J. 1969. A study of the homing habit of the limpet. *Anim. behav.*, *17* 330-339.

Cowell, E.B. and Crothers, J.H. 1970. On the occurrence of multiple rows of 'teeth' in the shell of the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.*, *50* 1101-1111.

Crothers, J.H. 1966. Dale Fort Marine Fauna (second edition). *Fld. Studs.*, 2 suppl., p.169.

Crothers, J.H. 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. *J. mar. biol. Ass. U.K.*, *51* 623-639.

Crothers, J.H. 1974. On variation in the shell of the dog-whelk *Nucella lapillus* L. I. Pembrokeshire *Fld. Studs.*, *4* 39-60.

Dame, R.T. 1976. Energy flow in an intertidal oyster population. *Estuar. Coast. Mar. Sci.*, *4* 243-253.

Das, S.M. and Seshappa, G. 1948. A contribution to the biology of *Patella* on population distribution and sex proportions in *Patella vulgata* L. at Cullercoats, England. *Proc. zool. Soc. Lond.*, *117* 411-423.

Davies, P.S. 1966. A constant pressure respirometer for medium sized animals. *Oikos.*, *17* 108-112.

Dodd, J.M. 1957. Artificial fertilisation, larval development and metamorphosis in *Patella vulgata* L. and *Patella coerulea* L. *Publ. staz. zool. Napoli.*, *29* 172-186.

Dodgson, K.S. and Spencer, B. 1954. Studies on sulphatases. 7. A preliminary account of the glycosulphatase of *Littorina littorea*. *Biochem. J.*, *57* 310-315.

Dongen, A. van. 1956. The preference of *Littorina obtusata* for *Fucaceae*. *Arch. néerl. Zool.*, *11* 373-386.

Dunn, A. and Arditti, J. 1963. *Experimental Physiology*. New York: Holt, Rinehart & Winston Inc., p.312.

Engelmann, M.D. 1961. The rate of soil arthropods in the energetics of an old field community. *Ecol. Monogr.*, *31* 221-238.

Engelmann, M.D. 1966. Energetics, terrestrial field studies and animal productivity. *Advances in Ecological Research*, *3* 73-115.

Feare, C.J. 1969. The dynamics of a population of dog-whelks (*Thais lapillus*). Ph.D. thesis, University of Leeds.

Feare, C.J. 1970. Aspects of the ecology of an exposed shore population of dog-whelks *Nucella lapillus* L. *Oecologia (Berl.)*, *5* 1-18.

Feare, C.J. 1971. The adaptive significance of aggregation behaviour in the dog-whelk *Nucella lapillus* L. *Oecologia (Berl.)*, *7* 117-126.

Fischer-Piette, E. 1939. Sur la croissance et la longévité de *Patella vulgata* L. en fonction du milieu. *J. conch. Paris*, *83* 303-310.

Fischer-Piette, E. 1941. Croissance, taille maxima et longévité possible de quelques animaux intocotideaux en fonction du milieu. *Annls. Inst. océanogro. Monaco*, *21* 1-28.

Fischer-Piette, E. 1946. Review of Biology of *Patella* in Great Britain, par J. Orton, *Nature*, *158* 173, 1946. *J. Conchyliol.*, *87* 83-84.

Fischer-Piette, E. 1948. Sur les éléments de prospérité des patelles et sur leur spécificité. *J. conch. Paris*, *83* 45-96.

Fretter, V. 1953. The transference of sperm from male to female prosobranch, with reference also to the pyramidellids. *Proc. Linn. Soc. Lond.*, sess. 164, 217-224.

Fretter, V. and Graham, A. 1962. British prosobranch molluscs. *Ray Society, London*, p.755.

Golley, F.B. 1961. Energy values of ecological materials. *Ecology*, *42* 581-584.

Golley, F.B. and Gentry, J.B. 1964. Bioenergetics of the southern harvester ant, *Pogonomyomex badius*. *Ecology*, *45* 217-225.

Gompel, M.M. 1937. Recherches sur la consommation d'oxygène de quelques animaux aquatiques littoreux. C.R. Acad. Sci. Paris, *205* 816-818.

Grahame, J. 1973. Assimilation efficiency of *Littorina littorea* L. (Gastropoda: Prosobranchiata). *J. Anim. Ecol.*, *42* 383-9.

Guiterman, J.D. 1970. The population biology of *Littorina obtusata*. Ph.D. thesis, University College of North Wales.

Hancock, D.A. 1960. The ecology of the molluscan enemies of the edible molluscs. *Proc. malac. Soc. Lond.*, *34* 123-144.

Harwood, J.E. and Kuyser, D.J. 1970. Some aspects of the phenolhypochlorite reaction as applied to ammonia analysis. *Water Research*, *4* 501-515.

Hatton, H. 1936. Observations sur l'habitat et sur la croissance de *Patella vulgata* L. *Bull. lab. marit. Dinard*, *15* 17-20.

Hatton, H. 1938. Essais de bionomie explicative sur quelques espèces intercotidales d'Alques et d'animaux. *Annls. Inst. océanogr. Monaco*, *17* 241-348.

Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno. meml. Hosp.*, *9(2)* 1-110.

Hughes, R.N. 1970. An energy budget for a tidal flat population of the bivalve *Scrobicularia plana* (Da Costa). *J. Anim. Ecol.*, *39* 357-381.

Hughes, R.N. 1971. Ecological energetics of the keyhole limpet, *Fissurella barbadensis* Gmelin. *J. exp. mar. biol.*, *6* 167-178.

Hughes, R.N. 1971. Ecological energetics of *Nerita* (Archaegastropoda, Nerititacea) populations on Barbados, West Indies. *Mar. Biol.*, *11* 12-22.

Ivlev, V.S. 1935. Eine mikromethode zur bestimmung des Kaloriengehalts von näkratoffen. *Biochem. Z.*, *275* 49-55.

Jensen, A.S. 1951. Do the *Naticidae* (Gastropoda, Prosobranchia) drill by chemical or mechanical means ? *Vidensk. Meddr. dansk.* naturh. Foren., *113* 251-261.

Jones, N.S. 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proc. Trans. Lpool. biol. Soc.*, *56* 60-77.

Ketchum B.H. and Redford, A.C. 1949. Some physical and chemical characteristics of algae grown in mass culture. *J. cell. Comp. Physiol.*, *33* 281-300.

Kuenzler, E.J. 1961. Structure and ecology flow of a mussel population in a Georgia salt marsh. *Limnol. Oceanogr.*, *6* 191-204.

Lack, D. 1954. The natural regulation of animal numbers. Oxford: Oxford University Press.

Largen, M.J. 1967. The influence of water temperature upon the life of the dog-whelk *Thais lapillus* (Gastropoda: Prosobranchia). *J. anim. Ecol.*, *36* 207-214.

Lebour, M.V. 1936. Notes on the eggs and larvae of some Plymouth prosobranchs. *J. mar. biol. Ass. U.K.*, *20* 547-565.

Lewis, J.R. and Bowman, R.S. 1975. Local habitat induced variations in the population dynamics of *Patella vulgata* L. *J. exp. mar. Biol. Ecol.*, *17* 165-203.

Lindemann, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, *23* 399-410.

Linke, O. 1933. Morphologie und physiologie des genitalapparates der Nordsee littorinen. *Wiss. Meeresuntersud. Abt. Helgoland*, *19 Nr.5* 3-52.

Macfadyen, A. 1963. Animal Ecology: Aims and Methods. 2nd edn. London.

MacNeil, S. and Lawton, J.H. 1970. Animal production and respiration in annimal populations. *Nature*, *225* 472-474.

Mann, K.H. 1964. The pattern of energy flow in the fresh and invertebrate fauna of the river Thames. *Verh. int. Verein. theor. angew. Limnol.*, *15* 485-495.

Mann, K.H. 1965. Energy transformations by a population of fish in the river Thames. *J. anim. Ecol.*, *34* 253-275.

Moore, H.B. 1931. The systematic value of molluscan faeces. *Proc. malac. Soc. Lond.*, *29* 281-290.

Moore, H.B. 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *J. mar. biol. Ass. U.K.*, *21* 61-89.

Moore, H.B. 1938a. The biology of *Purpura lapillus*. II. Growth. *J. mar. biol. Ass. U.K.*, *23* 57-66.

Moore, H.B. 1938b. The biology of *Purpura lapillus*. III. Life history and relation to environmental factors. *J. mar. biol. Ass. U.K.*, *23* 67-74.

Moore, H.B. 1938c. Algal-production and food requirements of a limpet. *Proc. malac. Soc. Lond.*, 23 117-118.

Nicholson, A.J. 1957. The self-adjustment of populations to change. *Cold Spring Harb. Symp. quant. Biol.*, 22 153-172.

Odum, E.P. 1963. *Ecology*. New York.

Odum, E.P. and Smalley, A.E. 1959. Comparison of population energy flow of a herbivorous and deposit-feeding invertebrate in a salt marsh ecosystem. *Proc. nat. Acad. Sci. U.S.A.*, 45 617-22.

Odum, E.P., Connell, C.E. and Davenport, L.B. 1962. Population energy flow of three primary consumer components of old-field ecosystems. *Ecology*, 43 88-96.

Orton, J.H. 1920. Sex-phenomena in the common limpet (*Patella vulgata*). *Nature*, Lond., 104 373.

Orton, J.H. 1928. Observations on *Patella vulgata*. II. Rate of shell growth. J. mar. biol. Ass. U.K., 15 863-874.

Orton, J.H., Southward, A.J. and Dodd, J.M. 1956. Studies on the biology of limpets. II. The breeding of *Patella vulgata* L. in Britain. *J. mar. biol. Ass. U.K.*, 35 149-176.

Paine, R.T. 1965. Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology*, 46 603-619.

Paine, R.T. 1971. Energy flow in a natural population of the herbivorous gastropod *Tegula funebralis*. *Limnol. Oceanogr.*, 16 86-98.

Pelseneer, P. 1935. Essai d'éthologie zoologique d'après l'étude des mollusques. *Publs. Fond. Agathon de Potter*, 1 1-662.

Pettitt, C. 1975. A review of the predators of *Littorina*, especially those of *L. saxatilis* (Olivz) (Gastropoda: Prosobranchia). *J. Conch. Lond.*, 28 343-357.

Petrusewicz, K. 1967. Suggested list of more important concepts in productivity studies (definitions and symbols). Secondary Productivity of Terrestrial Ecosystems, 1. (ed. by K. Petrusewicz) 51-82. Warsaw and Cracow.

Phillipson, J. 1962. Respirometry and the study of energy turnover in natural systems with particular reference to harvest spiders. (Phalangiidae). Oikos, 13 311-322.

Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos, 15 130-139

Phillipson, J. 1966. Ecological Energetics. The Institute of Biology's Studies in Biology, No.1. London.

Prus, T. 1970. Calorific value of animals as an element of bioenergetics investigations. Pol. Arch. Hydrobiol., 17(30), No.1/2, 183-199.

Ricker, W.E. (ed.) 1968. Methods for assessment of fish production in fresh waters. I.B.P. Handbook No.3. Oxford and Edinburgh.

Richman, S. 1958. The transformation of energy by Daphnia pulex. Ecol. Mongr., 28 275-291.

Russell, E.S. 1909. The growth of the shell of Patella vulgata. Proc. zool. Soc. Lond., 79 235-253.

Sandeen, M.I., Stephens, G.C. and Brown, F.A. 1954. Persistent daily and tidal rhythms of oxygen consumption in two species of marine snails. Physiol. Zool., 27 350-356.

Sandison, E.E. 1966. The oxygen consumption of some intertidal gastropods in relation to zonation. J. Zool. Lond., 149 163-173.

Scholander, P.F. 1942. Volumetric microrespirometers. Rev. Sci. Instrum., 13 32-33.

Slobodokin, L.B. 1962. Energy in animal ecology. Adv. Ecol. Res., 1 69-101.

Smalley, A.E. 1960. Energy flow of a salt marsh grasshopper population. Ecology, 41 672-677.

Smith, F.G.W. 1935. The development of Patella vulgata. Phil. Trans. R. Soc. B., 225 95-125.

Solórzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Oceanogr., 14 799-801.

Southward, A.J. 1953. The ecology of some rocky shores in the south of the Isle of Man. *Proc. Lpool. Biol. Soc.*, *59* 1-50.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, 43 614-624.

Tenore, K.R., Goldman, I.C. and Clarner, I.P. 1973. The food chain dynamics of the oyster, clam and mussel in an aquaculture food chain. *J. exp. mar. Biol. Ecol.*, *12* 157-165.

Thorsen, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komn. Havundersøg. KGh ser. Plankton.*, *4* 1-523.

Trevallion, A. 1971. Studies on *Tellina tenuis* (Da Costa). III. Aspects of general biology and energy flow. *J. exp. mar. biol. Ecol.*, *7* 95-122.

Vinogradov, A.P. 1953. The elementary chemical composition of marine organisms. *Mem. Sears. Found. Mar. Res.*, *2* p.647

Ward, J. 1966. Distribution and growth of the keyhole limpet *Fissurella barbadensis* (Gmelin). *Bull. mar. Sci. Gulf Caribb.*, *16* 685-695.

Welch, H.E. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. *Ecology*, *49* 755-759.

Winberg, G.G. 1956. Rate of metabolism and food requirements of fish. *Fish. Res. Bd. Can. Translation series*, *194* 1-202.

Zeuthen, E. 1953. Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.*, *28* 1-12.

APPENDIX 1

Micro-bomb calorimeter: A Phillipson oxygen micro-bomb calorimeter produced by Gentry Instruments, serial no. 239, and a potentiometer recorder, Unicam AR 35, were used. Phillipson (1964) describes the design and operation of the calorimeter.

Gilson respirometer: The respirometer was a modified Gilson G.P.14 which is a constant pressure type. A refrigeration unit was added to enable the experiments to be carried out below room temperature. Dunn and Arditti (1968) describe the design and operation of a Gilson respirometer.

APPENDIX 2

Aspects of Homing in the Limpet, Patella vulgata L.

R.G. Hartnoll and J.R. Wright

Homing is a widespread phenomenon in limpets: it occurs in the pulmonate siphonarian limpets (see Cook & Cook 1975 and Thomas 1973 for full references), and in prosobranch limpets of both the Acmaeidae (Galbraith 1965, Hewatt 1940) and the Patellidae (see Cook et al. 1969 for references). This ability is an important component of the limpet life style, and is a necessary consequence of the need both to forage afield for the algae on which they graze, and yet to have a home site where the shell of the limpet accurately matches the contours of the rock. Since they lack an operculum limpets depend upon the exactness of this match to restrict desiccation. A proportion of limpets admittedly change their home site from time to time (Jones 1948, Lewis 1954), more commonly amongst those frequenting smooth surfaces (Jones 1948), but even here homing is distinctly the normal behaviour.

This study deals with patellid limpets, two aspects of whose homing behaviour have previously attracted attention. One is the mechanism by which homing is accomplished (Cook et al. 1969, Funke 1968). This was not investigated, and will not be considered further except to note that the consensus is now that chemical trails laid on the rock must be involved. The topic of this study is the timing, distance and speed of the foraging movements which culminate in a return to the home site. Previous observations on speed and distance are sparse, and will be dealt with in discussion, but the earlier studies on the timing of movement in Patella vulgata reveal some striking variations. Orton (1929) summarized previous work and added his own from the Plymouth area, concluding that whilst some foraging occurred when the limpets were uncovered in conditions of shade or humidity, the bulk took place when they were immersed at high water.

Jones (1948) and Cook et al. (1969) recorded similar behaviour in the Isle of Man, but in Alderney Cook et al. found that foraging was limited to nocturnal low waters. Laboratory studies on material from Roscoff (Funke 1968) revealed a similar preference to move in darkness, but with a less pronounced preference for low water. None of these earlier studies included observation during nocturnal immersions, and in view of this and the surprising variations noted above, it was decided to make a further study of homing behaviour in some populations in the Isle of Man.

Methods

Observations were made at two sites in the Isle of Man, both situated at approximately mean tide level. One was on a smooth and fairly level ledge of carboniferous limestone at Derbyhaven, the second on the horizontal upper surface of a rough concrete jetty at Port Erin. At each site a small area containing fourteen limpets was selected. Each limpet was numbered on the side of the shell with waterproof paint, and a small dot, from which all measurements were taken, painted on the apex. At each site three bolts were fixed into the substrate in a roughly equilateral triangle, and their positions carefully determined. During subsequent observations the position of each limpet was calculated by triangulation after the distances from the apex to the three bolts had been measured. When the areas became immersed at high water observations were continued by diving both by day and night.

Results

Observations were made on seven occasions between June 12th and September 15th 1975, and consistent results were obtained from the two locations. During darkness no significant movement occurred, irrespective of whether the areas were immersed or uncovered. In daylight the limpets remained at their home sites whilst uncovered, but foraged once they became immersed. As soon as spray from the waves started to reach them regularly as the tide rose they began to move, they were at the maximum distance from home over the time of high water, and then returned home one or two hours before the area was uncovered again on the ebb. Table I shows that the proportion of limpets foraging on each occasion varied from 64% to 86%, with a mean of 76%, so that on any one day at that time of year only some three-quarters of the population feed. The greatest distance reached from the home site was 1.21 m, and the mean distance 0.41 ± 0.09 m. The total distances travelled on each excursion will have been rather more than twice the above figures because of the meandering path taken during the feeding period. A detailed analysis of the movements on the Derbyhaven site on June 12th is presented in Table II and Figs. 1 & 2. Movement began as soon as the site was submerged, and the limpets moved fairly directly to the feeding areas at a mean speed of $107 \pm 44 \times 10^{-6}$ m sec^{-1}. By one and a half hours after immersion the limpets were near the maximum distance from their home sites, and for some two hours they grazed on growths of algae and diatoms, moving slowly at a mean of $14 \pm 6 \times 10^{-6}$ m sec^{-1}. They then returned home rapidly, with a mean speed of $92 \pm 35 \times 10^{-6}$ m sec^{-1}, and all were at their home sites at least an hour before the area was uncovered by the falling tide.

The survey of September 15th clearly demonstrated the interaction of the tidal and light / dark cycles in regulating the foraging activity. On that occasion the area was immersed at 18.30, it became dark at 20.30, and high water was at 21.30. All limpets were at their home sites until immersion, but at 19.30 43% had moved to a mean distance of 0.36 m. However, at 21.30 all had returned to their home sites, whereas if darkness had not intervened they would at that stage of the tidal cycle have been feeding at the maximum distance from home.

Discussion

Three aspects of foraging behaviour will be considered in turn - the timing and control of movement, the speeds involved and the distances travelled.

Fig.1. Plots of the movements of individual limpets at the Derbyhaven site during the daylight immersion of 12 vi 75.

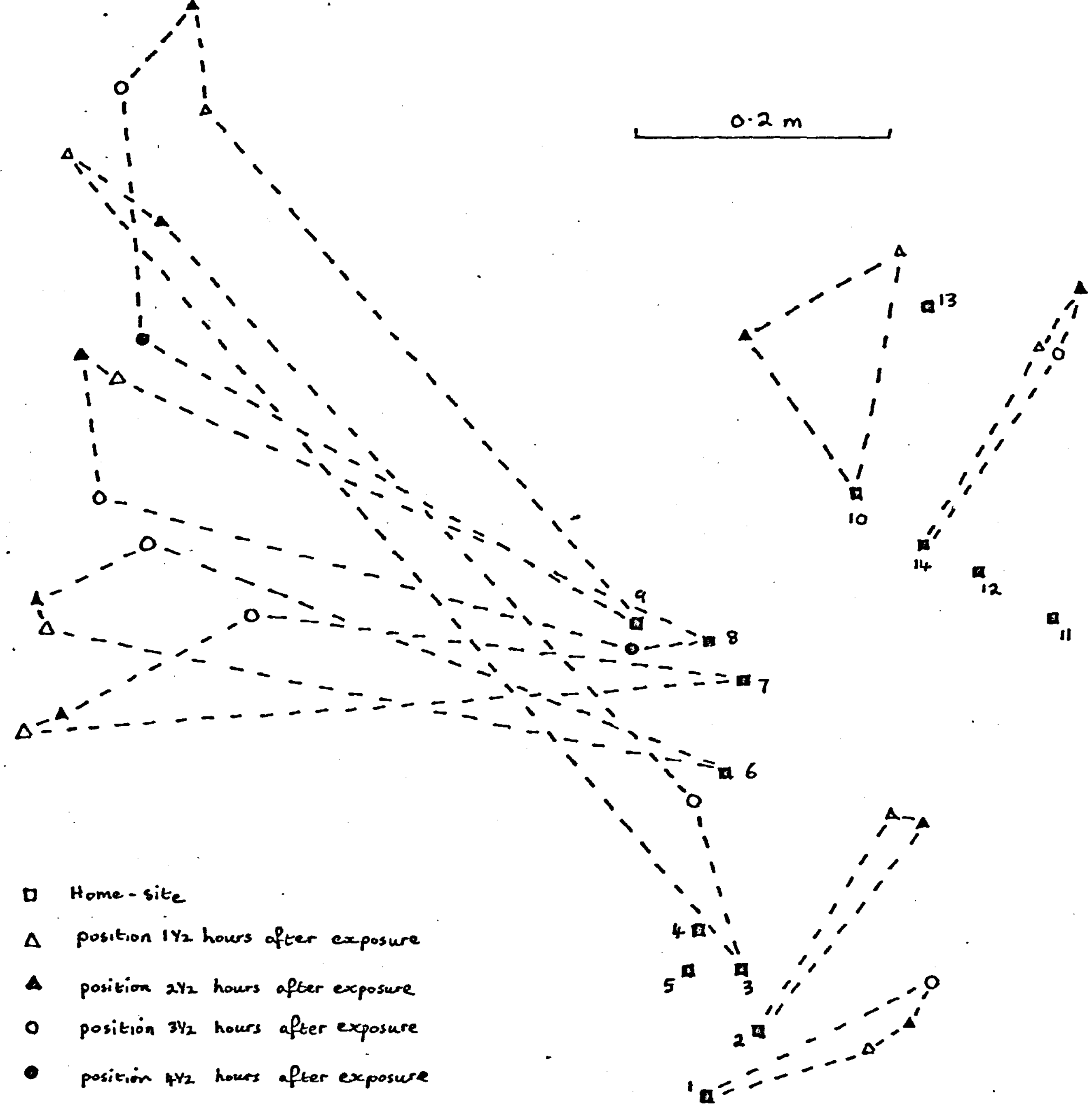

0·2 m
1
2
3
4
5
6
7
8
9
10
11
12
13
14
□ Home-site
△ position 1½ hours after exposure
▲ position 2½ hours after exposure
○ position 3½ hours after exposure
● position 4½ hours after exposure

Fig.2. The average speed of movement (solid line) and distance from home site (broken line) for the foraging limpets on the Derbyhaven. site during the daylight immersion of 12 vi 75.

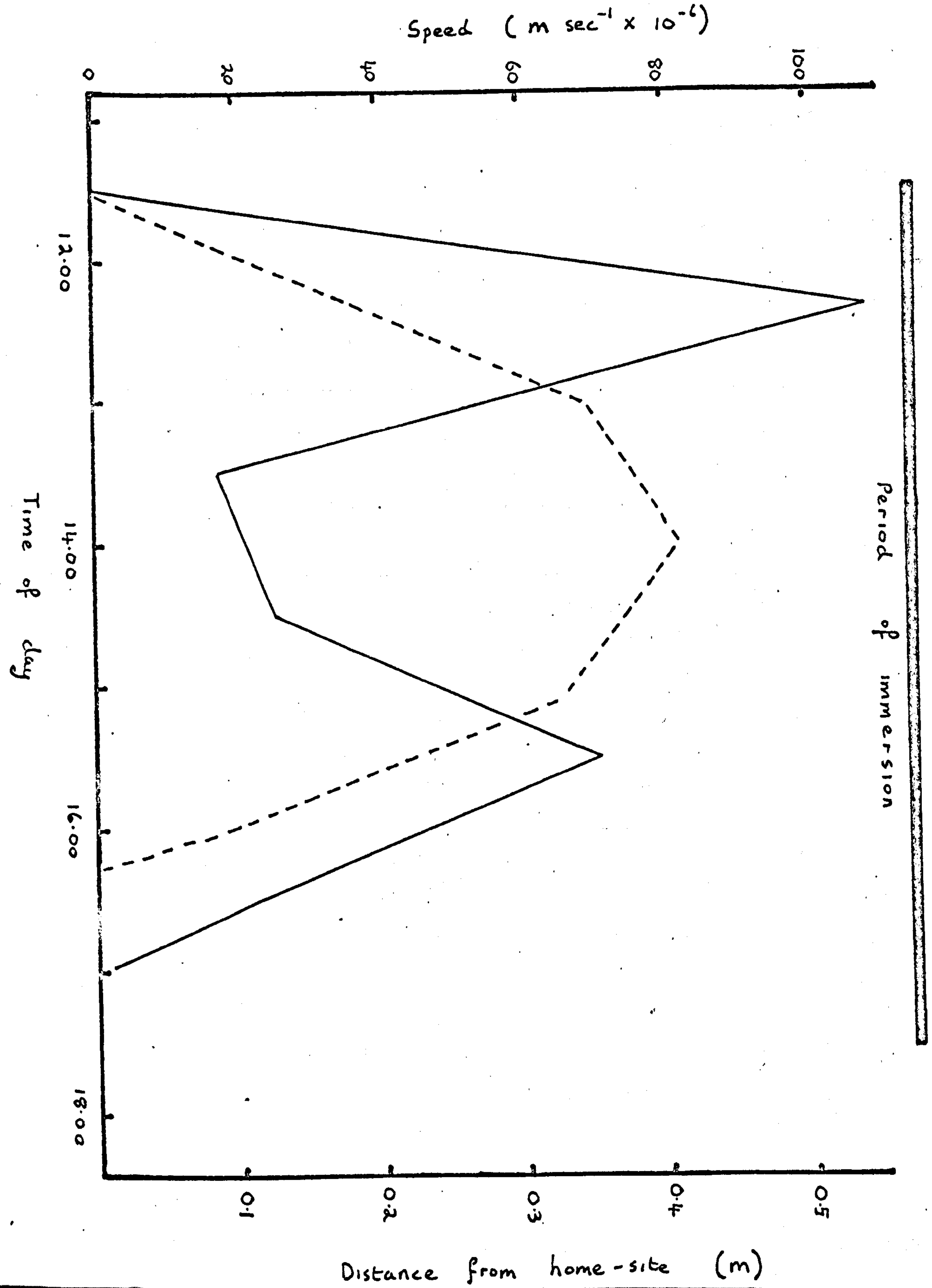

Speed (m sec^{-1} x 10^{-6})
0
20
40
60
80
100
12.00
14.00
16.00
18.00
Time of day
Period of immersion
0.1
0.2
0.3
0.4
0.5
Distance from home-site (m)

Table I Patella vulgata: An analysis of the incidence and extent of foraging movements in the Isle of Man and in Alderney (for the latter using data from figures in Cook et al. 1969)

Location	Number observed	Number moving	Percentage moving	Maximum movement (m)	Mean movement (m)
Derbyhaven 12.6.75	14	9	64	0.84	0.44 ± 0.18
Port Erin 7.8.75	14	12	86	1.21	0.39 ± 0.21
Port Erin 13.8.75	14	11	79	1.00	0.37 ± 0.19
Port Erin 4.9.75	13	9	69	0.86	0.44 ± 0.19
Total: Isle of Man	55	41	76	1.21	0.41 ± 0.09
Alderney	-	21	-	0.36	0.17 ± 0.03

Table II Patella vulgata: Analysis of the movement of individual limpets at the Derbyhaven site on 12th June 1975 (as plotted in Fig. 1)

No. of limpet	Maximum distance from home site (m)	Outward speed ($m\ sec^{-1} \times 10^{-6}$)	Feeding speed ($m\ sec^{-1} \times 10^{-6}$)	Return speed ($m\ sec^{-1} \times 10^{-6}$)
1	0.20	37.5	9.7	55.6
2	0.21	55.6	8.3	44.5
3	0.84	187.5	25.0	173.6
6	0.56	150.0	9.7	108.3
7	0.57	159.7	8.3	109.7
8	0.55	143.1	9.7	122.2
9	0.60	136.0	23.6	125.0
10	0.19	52.8	-	41.7
14	0.24	43.1	15.3	44.4
Mean	0.44 ± 0.18	107.2 ± 44.4	13.7 ± 5.6	91.7 ± 35.4

This study confirms the earlier observations on the timing of foraging in Manx populations of Patella vulgata, but in doing so serves only to accentuate the behavioural differences within the species. On the one hand the studies at Plymouth (Orton 1929) and the Isle of Man show that foraging occurs when the limpets are covered at high water, and in the Isle of Man at least only during daylight immersions. In contrast, observations at Alderney (Cook et al. 1969) and laboratory work on material from Roscoff (Funke 1968) showed that movement is predominantly at night when the limpets were uncovered at low tide. At Alderney the high-shore populations showed some movement when immersed, but the mid-shore limpets, which are comparable to those studied in the Isle of Man, moved little except when uncovered. The onset and cessation of movement were clearly correlated with sunset and sunrise respectively (Cook et al. 1969, Fig. 2), again the converse of that observed in the Isle of Man. There is no obvious explanation for these intraspecific differences, but there is possibly a consistent geographical trend, and further investigation of this would be of interest.

Observations on other prosobranchs reveal yet more diversity. In Alderney Patella depressa had a pattern of movement resembling that of P. vulgata, but the low-shore P. aspera had no clear periodicity (Cook et al. 1969). In captivity the Mediterranean P. caerulea foraged at nocturnal high water (Funke 1968), whilst in the field the South African P. granularis did so at nocturnal low water (Stephenson 1936). Acmaea scabra (Hewatt 1940) and Acmaea digitalis and Lottia gigantea (Galbraith 1965) all forage during diurnal high water. The only unifying feature in the prosobranchs is that there is one relatively long period of feeding activity each day, and to ensure protection from desiccation this is either by night, or at high water, or occasionally both. All of the pulmonate limpets which have been studied show a quite different pattern of movement (Cook 1969, 1971, Ohgushi 1954, Thomas 1973). There are relatively brief periods of activity whilst the limpets are being covered by the rising tide, and again as the falling tide uncovers them, but they are inactive at high and low water. At least some of the species forage both by day and night. This limitation of activity to the periods of semi-submergence correlates with the basically air breathing respiration of the pulmonates.

Movement in Patella vulgata must be controlled ultimately by the tidal and light / dark cycles, either as a direct response to the changing environment, or through intrinsic rhythms entrained by the environmental variables. Mostly the onset and cessation of movement in both the Isle of Man and Alderney correlate with gross environmental changes - the coming of light or darkness, coverage of the area by the tide, or the fall in hydrostatic pressure as the tide falls - so that the role of any intrinsic rhythms is not apparent. However, in Alderney the homeward movement commences well before the rising tide reaches the limpets, indicating a rhythmic component.

There are few other observations on the speed of limpet movement. Cook et al. (1969) record a maximum of 250 x 10^{-6} m sec^{-1} for Patella vulgata over a five minute period, and this is a better estimate of the maximum speed than the 188 x 10^{-6} m sec^{-1} of the present study based on a one hour observation. The only record of another species is for Siphonaria pectinata, which can average 560 x 10^{-6} m sec^{-1} for five minutes (Thomas 1973).

The distances travelled from the home site are somewhat better documented. From the figures in Cook et al. (1969) it can be determined that Patella vulgata in Alderney moves a maximum of 0.36 m with a mean of 0.17 ± 0.03 m. These journeys are significantly shorter than those made by the Manx specimens, who perhaps move further because they do so whilst covered by the tide. The records for other species form no consistent pattern. In South Africa Patella granularis moves up to 1.5 m, but P. longicosta and P. cochlea move 0.1 m or less (Stephenson 1936).

Acmaea digitalis and *Lottia gigantea* travel on average 0.13 m and 0.08 m respectively (Galbraith 1965), and *Acmaea scabra* up to 0.4 m with an average of 0.19 m (Hewatt 1940). *Siphonaria pectinata* can move up to 0.75 m, but 0.1 m or less is normal (Thomas 1973). On the basis of this rather scattered information *Patella vulgata* in the Isle of Man is one of the most mobile of limpets.

Summary

In two populations of *Patella vulgata* in the Isle of Man foraging activity is restricted to daytime high waters, with about 75% of the population foraging on any one day. Movement commences as the tide covers the limpets, and they travel an average of 0.4 m from their home sites to which they return at least an hour before the falling tide exposes them again. The mean speed on the outward and return journeys is around 100×10^{-6} m sec^{-1}, and during the intervening browsing period about 14×10^{-6} m sec^{-1}. This behaviour contrasts with that of the same species in Alderney, where foraging is limited to nocturnal low waters; there is possibly a geographical trend in behaviour. *Patella vulgata*, especially in the Isle of Man, is one of the more mobile limpets.

Acknowledgements

We offer our sincere thanks to M. Bates, R. Dalley and D. Morris for their help with the diving.

References

Cook, A., Bamford, O.S., Freeman, J.D.B. and Teideman, D.J. (1969). A study of the homing habit of the limpet. *Anim. Behav.*, *17*, 330-339.

Cook, S.B. (1969). Experiments on homing in the limpet *Siphonaria normalis*. *Anim. Behav.*, *17*, 679-682.

Cook, S.B. (1971). A study of homing behavior in the limpet *Siphonaria alternata*. *Biol. Bull.*, *141*, 449-457.

Cook, S.B. and Cook, C.B. (1975). Directionality in the trail-following response of the pulmonate limpet *Siphonaria alternata*. *Mar. Behav. Physiol.*, *3*, 147-155.

Funke, W. (1968). Heimfindevermogen und Ortstreue bei *Patella* L. (Gastropoda, Prosobranchia). *Oecologia* (Berl.), *2*, 19-142.

Galbraith, R.T. (1963). Homing behaviour in the limpets *Acmaea digitalis* and *Lottia gigantea*. *Am. Midl. Nat.*, *74*, 245-246.

Hewatt, W.G. (1940). Observations on the homing limpet *Acmaea scabra* Gould. *Am. Midl. Nat.*, *24*, 205-208.

Jones, N.S. (1948). Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proc. Trans. Lpool Biol. Soc.*, *56*, 60-77.

Lewis, J.R. (1954). Observations on a high level population of limpets. *J. anim. Ecol.*, *23*, 85-100.

Ohgushi, R. (1954). Ethological studies on the intertidal limpets. 1. On the tidal rhythmic activities of two species of limpets. *Jap. J. Ecol.*, *4*, 120 (in Japanese with English summary).

Orton, J.H. (1929). Observations on *Patella vulgata* L. 3. Habitat and habits. *J. mar. biol. Ass. U.K.*, *16*, 277-288.

Stephenson, T.A. (1936). The marine ecology of the South African coast, with special reference to the habits of limpets. *Proc. Linn. Soc. Lond.*, *148*, 74-79.

Thomas, R.F. (1973). Homing behavior and movement rhythms in the pulmonate limpet *Siphonaria pectinata* Linnaeus. *Proc. malac. Soc. Lond.*, *40*, 303-311.