ECOLOGICAL STUDIES ON THE LIMPET *CELLANA RADIATA* (BORN), AT ANJUNA, GOA.

THESIS SUBMITTED TO GOA UNIVERSITY
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IN
MARINE SCIENCE

BY

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STATEMENT

I hereby state that this thesis for the Ph.D degree on "THE ECOLOGY OF THE LIMPET *Cellana radiata* (BORN) AT ANJUNA, GOA." is my original contribution and that the thesis and any part thereof has not been previously submitted for the award of any degree, diploma of any University or Institute. To the best of my knowledge, the present study is the first comprehensive study of its kind from this area.

The literature pertaining to the problem investigated has been duly cited. Facilities availed from other sources are duly acknowledged.

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CERTIFICATE

This is to certify that the thesis entitled " THE ECOLOGY OF THE LIMPET *Cellana radiata* (BORN) AT ANJUNA, GOA. " submitted by Smt. A. BALAMANI for the award of the degree of Doctor of Philosophy in MARINE SCIENCE is based on the results of investigations carried out by the candidate under my supervision. The thesis or any part thereof has not been previously submitted for any other degree or diploma of any University or Institute. The material obtained from other sources has been duly acknowledged in the thesis.

25/1/96

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CHAPTER I

INTRODUCTION

Biological communities are an intricately intertwined part of our ecosystem. Their functioning can be understood by studying either the community as a whole or its component species populations separately. The latter approach unveils their complexity and is useful for developing simulation models of natural ecosystems. The intertidal zone has been the arena for many field studies, primarily due to their diversity and easy accessibility.

Among the rocky intertidal inhabitants, one of the most conspicuous and successful group are the limpets. These molluscs have a shell, consisting of a low wide cone with a more or less central apex and large rounded or oval aperture, filled with a broad foot. This animal, unlike other gastropods, cannot withdraw into the shell but, instead, has developed habits like clamping its foot and shell edge to rocks or other firm substratum.

1.1 ECOLOGY OF LIMPETS

Limpets show a cosmopolitan distribution invading both the marine as well as the fresh water regimes. They vary in their size, shape, structure and color pattern. Their ecology has been extensively reviewed by Branch (1981). Limpets, inhabiting the intertidal regime, are subjected to many physiological stresses. The physical factors that affect intertidal organisms are temperature, desiccation, salinity and wave action. The first two factors are more critical since they determine the limits of distribution of the organisms in the intertidal zone.

1.1.1 PHYSICAL FACTORS

The temperature tolerances of littoral gastropods have been studied by several investigators (Davies, 1969; Vermeij, 1971; Wolcott, 1973; Simpson, 1976). Limpets are poor regulators of temperature due to increased degree of body contact with the substratum (Vermeij, 1971). Absorption or heat uptake mainly depends on the area exposed, limpet orientation and absorptivity of its surface (Branch, 1981). The entire surface area of the conical shell is available for reradiation which increases with increasing surface irregularity (Vermeij, 1973). Though field temperatures do not generally exceed thermal tolerance of limpets (Wolcott, 1973), there are several reports on the death and disappearance of limpets from the upper shore due to extreme temperatures (Walker, 1972; Simpson, 1976). One of the physical effects of increasing temperature is an increase in evaporation rates, dessication and metabolism (Branch, 1981). In the sub-antarctic limpet, *Nacella concinna*, the intertidal population migrates downshore during winter when temperature reaches -20°C (Walker, 1972).

Dessication is the most important factor that affect limpets during tidal exposure since it determines their upper limits (Wolcott, 1973; Underwood, 1979; Branch, 1981). It causes detrimental reduction in the uptake of oxygen. Shotwell (1950) observed that smaller species of *Acmaea* sp., *Notoacmaea scutum* and *Collisella pelta* occurred higher on the shore than its larger counterparts due to a higher proportion of extra visceral water (between body and shell). Shell shape can also influence rate of water loss. Limpets at higher tidal levels have a taller and more domed shell (Rao & Ganapati, 1971a; Walker, 1972; Bannister, 1975). A taller shell also aids in reduction of desiccation (Vermeij, 1973; Davies, 1969). To avoid desiccation, limpets migrate upwards during wetter conditions (Frank, 1965; Haven, 1971; Choat, 1977) and downwards during drier conditions (Branch, 1975; Lewis, 1954). Homing is also considered to be an adaptation to desiccation.

Organisms inhabiting the intertidal region are subject to varying degrees of wave action, particularly on rocky shores where zonation patterns are evident (Lewis,1964). In rocky habitats, organisms find refuge in the crevices and depressions in the rocks to prevent dislodgement due to high wave action (Emson & Faller-Fritch, 1976). Wave action is also responsible for limiting the distribution of organisms in rocky shores with organisms shifting further upshore with increasing wave action (Lewis, 1968).

The only defence limpets have against changing salinities is to clamp their shell tightly to the substratum, thus temporarily excluding the external medium. Rao and Ganapati (1972) reported that *Cellana radiata* is temporarily tolerant to salinities between 20% and 37%. Experimental studies have shown that when uncovered during low tides, limpets react to splashes of sea water by raising their shells from their position assumed during tight closure (Arnold, 1957). Tolerances to salinities are different in high and low shore limpets. *Patella lusitanica*, a high shore species was less tolerant to salinity variations than *P. coerulea*, a low shore species (Bannister, 1970). Salinity does not however fluctuate widely enough to limit their distribution (Wolcott, 1973; Simpson, 1976).

1.1.2 HOMING

Homing to a fixed scar is well documented in limpets and has evoked considerable interest. There are many variations between species and within species in the rigidity of homing behaviour. The proportion of the population homing, can be influenced by size of animals, the texture and stability of the rock, availability of food and the amount of desiccation (Branch, 1981). Though there are numerous reports on homing by limpets the mechanism has not been clearly understood. In general, small individuals do not home, territorial species home rigidly and homing is more precise in high shore species. There are however low shore and even subtidal species that have well developed scars and homing behaviour suggesting that desiccation is not the only deciding factor. The advantage of homing could be a reduction in mortality due to dessication (Lewis, 1954; Davies 1969) or an even dispersion in the distribution of limpets (Aitken, 1962; Underwood, 1977).

1.1.3 POPULATION STUDIES

These studies encompasses not only population abundance and age structure but several other life history traits such as birth rates, death rates, longevity, mode of reproduction, partitioning of energy resources, etc.. These are necessary to understand the population dynamics of species, which provides a rationale basis to explain changes in their density taking into account the role of the environment. Many authors have investigated the life history characteristics of different species to unravel common patterns. Attempts to analyse these differences in species is compounded since it is difficult to pinpoint whether these exist due to habitats, the species or due to an interaction between the two (Fletcher, 1984a).

Studies on intertidal gastropods especially limpets are abundant and have been reviewed by Underwood (1979) and Branch (1981). These studies have been restricted to *Patella vulgata* (Lewis and Bowman, 1975; Thompson, 1979), *Acmaea scabra* (Sutherland, 1970, 1972), *P. granularis* (Branch, 1976), *Notoacmaea petterdi* (Creese, 1980) and *Cellana tramoserica* (Fletcher, 1984a). The growth and population dynamics of these species vary widely among different habitats and are attributed to intra/interspecific competition and physical factors (Fletcher, 1984a) and variations in food supply (Bosman & Hockey, 1988). There are marked variations in the biological characteristics of *Cellana* spp. over small geographic distances and any attempt to comment on life history strategies must take into account such variablity of the biology of a single species (Fletcher, 1984a).

1.1.4 THE ENERGY BUDGET

Bioenergetics is a study which deals with the energy flow in an organism, population or an ecosystem. Information on the efficiencies of energy transformations can also be obtained. The units are standardised and hence data on the energy partitioning for various biological processes can be obtained.

The food consumed by an animal is basically diverted into two pathways, one is to maintain and increase its structure and secondly to drive its metabolic machinery. Feeding rates are chiefly influenced by temperature and salinity (Newell *et al.* 1971), time of day and season, past feeding history, body size, state of tide (Newell *et al.* 1971), size of prey (Broom, 1982), and nutritional quality of food (Carefoot, 1967). Consumption rates in limpets are difficult to estimate (Branch, 1981).

Energy lost as heat through metabolism is represented by respiration. Internal physiological factors which may effect the metabolism of animals are body size, age, developmental stage (Sutherland, 1972), nutritional state (Newell & Kofoed, 1977), state of stress (Calow, 1974), state of activity (Newell & Pye, 1971). External factors are diurnal and seasonal changes in temperature (Newell & Branch, 1980), relative humidity, state of tide (Sutherland, 1972; Branch 1981; Wright & Hartnoll 1981; Parry 1982a) and also tidal levels (Davies 1966; Rao 1980). The differential exposure to air complicates the effects of other environmental factors on the rate of oxygen consumption.

Energy rich waste products are eliminated from animals through faeces and urine. Faeces arise from food material which has not been digested or assimilated. Urine contains the nitrogenous products of catabolism with ammonia, urea and uric acid being the most common. The contribution of faeces and urine to the energy of the limpets is seldom measured. Faecal production has been correlated with growth rates (Branch, 1981). Wright and Hartnoll (1981) detemined the absorption efficiency of the limpet *P. vulgata* and then derived the energy of the faeces from the energy content of the consumed food. Faecal production in *C. tramoserica* is seasonal (Parry, 1977). Many organisms convert nitrogenous waste products such as ammonia into urea or uric acid before elimination (Duerr, 1967). The main excretory product in *Patella* is ammonia (Fretter & Graham, 1962).

The balance of absorbed energy left after expenditure on metabolism is mainly available for the production of somatic and reproductive tissues as well as storage products and secretion. Mucus secrètion and production is generally important not only for locomotion and adhesion but also for faecal production (Calow, 1974). Growth in gastropods is generally measured as a linear increment of the shell and converted to growth by using the relationship between weight and shell size. Estimating somatic growth from shell growth assumes a direct relationship between the two. However, shell growth can occur when there is no scope for tissue growth, such as during starvation, and the reverse also holds good (Palmer, 1981).

The cost of reproduction is referred to as reproductive effort. Methods of measurement ranges from the ratio of gonad to somatic weight (Fletcher, 1984b) to the ratio of gamete output to flesh weight (Branch, 1974a; 1975) to the proportion of annual production of gonad and gametes to assimilated energy (Parry, 1982b). There are basically two patterns of reproduction in limpets: species that breed continuously and intermittently. Species which live in an occassionally suitable environment will allocate more energy for reproduction while those which reproduce continuously will invest little towards reproduction, implying that optimal reproductive effort is determined by natural selection (Giesel, 1976).

1.2 REVIEW OF PREVIOUS WORK CARRIED OUT ON *C. radiata*

Among the earliest studies carried out on *C. radiata* along the Indian coast is that of Sukumaran and Krishnaswamy (1961) who investigated the response of limpets, collected from the rocks of Madras Harbour, to changes in salinity. The most detailed study on limpets has been carried out along the Waltair coast. Rao and Ganapati (1971a, b) described its ecology with special reference to their distribution and shell structural variations in relation to tidal levels. In addition, investigations on its resistance to variations in temperature, salinity and desiccation (Rao & Ganapati, 1972), reproductive cycle (Rao, 1973), spawning behaviour and larval development (Rao, 1975a), growth rates (Rao, 1976) and the effect of the body size and tidal rhythms on the respiratory metabolism (Rao, 1980) have also been reported.

Other studies include observations on feeding anatomy, histology of the digestive tract and digestive enzymes (Rao, 1975b) the relationship of the radula fraction and shell length at different tidal levels (Rao & Ganapati, 1967). Along the Saurashtra coast (West coast of India), seasonal variations in biochemical constituents of limpets and the response of limpets to desiccation and salinity stresses have been studied (Suryanarayan & Nair, 1976). Population density in the polluted waters of Porbandar have also been studied (Prasad and Mansuri, 1982). Seasonal variations in the biochemical constituents of *C. rota* at Ratnagiri have also been reported (Patil & Mane, 1982).

At Anjuna, results on a short term study on the spatial distribution of the limpet and intraspecific variations in shell characteristics have been reported (Balamani, 1990). The densities of prosobranch gastropods including *C. radiata* at several locations along the Goa coast were investigated by Coutinho (1993).

1.3 OBJECTIVES OF THE PRESENT STUDY

It is thus seen that information on limpets, particularly along the west coast, is limited. Reports on the quantitative abundance and distribution of *C. radiata* along the Goa coast are restricted to Balamani (1990) and Coutinho (1993). There are no reports on production estimates or reproductive effort for limpets along the Indian coast. It was thus proposed to carry out a long term study with the following objectives:

- To study the environmental conditions prevailing at Anjuna, the study area where the limpets, *Cellana radiata*, were observed.

- To study the variation in its shell characteristics.

- To study its diet through gut content analysis.

- To study its reproductive pattern.

- To investigate its movement pattern.

- To gain an insight into its population structure and successive changes with time and estimate its longevity.

- To analyse the seasonal variations in growth rates.
- To estimate its monthly, seasonal and annual somatic, gonadial and gamete biomass and production.
- To estimate its monthly, seasonal and annual respiratory losses.

CHAPTER II

MATERIALS AND METHODS

2.1 THE STUDY AREA

The study was conducted on the rocky shores of Anjuna (73°44'33"E and 15°35'10"N), Goa, along the west coast of India (Fig. 1). The beach has sandy and rocky regions. The study area selected. is a rocky platform running perpendicular to the shore and extending seawards upto 60m. The study was conducted between March 1992 and May 1995 and data presented mainly pertains to September 1993 - October 1994.

2.2 ENVIRONMENTAL PARAMETERS

Four environmental parameters *viz.* air temperature and sea surf temperature, salinity and dissolved oxygen were recorded every month, from September 1993 to October 1994, at Anjuna during the study period. Temperature readings were recorded to the nearest 0.2°C with a thermometer. Climatic data *viz.* the monthly maximum and minimum temperatures, rainfall and relative humidity were obtained from the Indian Meteorological Department, Panjim.

Water samples collected every month were analysed for its salinity by the Mohr-Knudsen method adopted from Grasshoff *et al.*

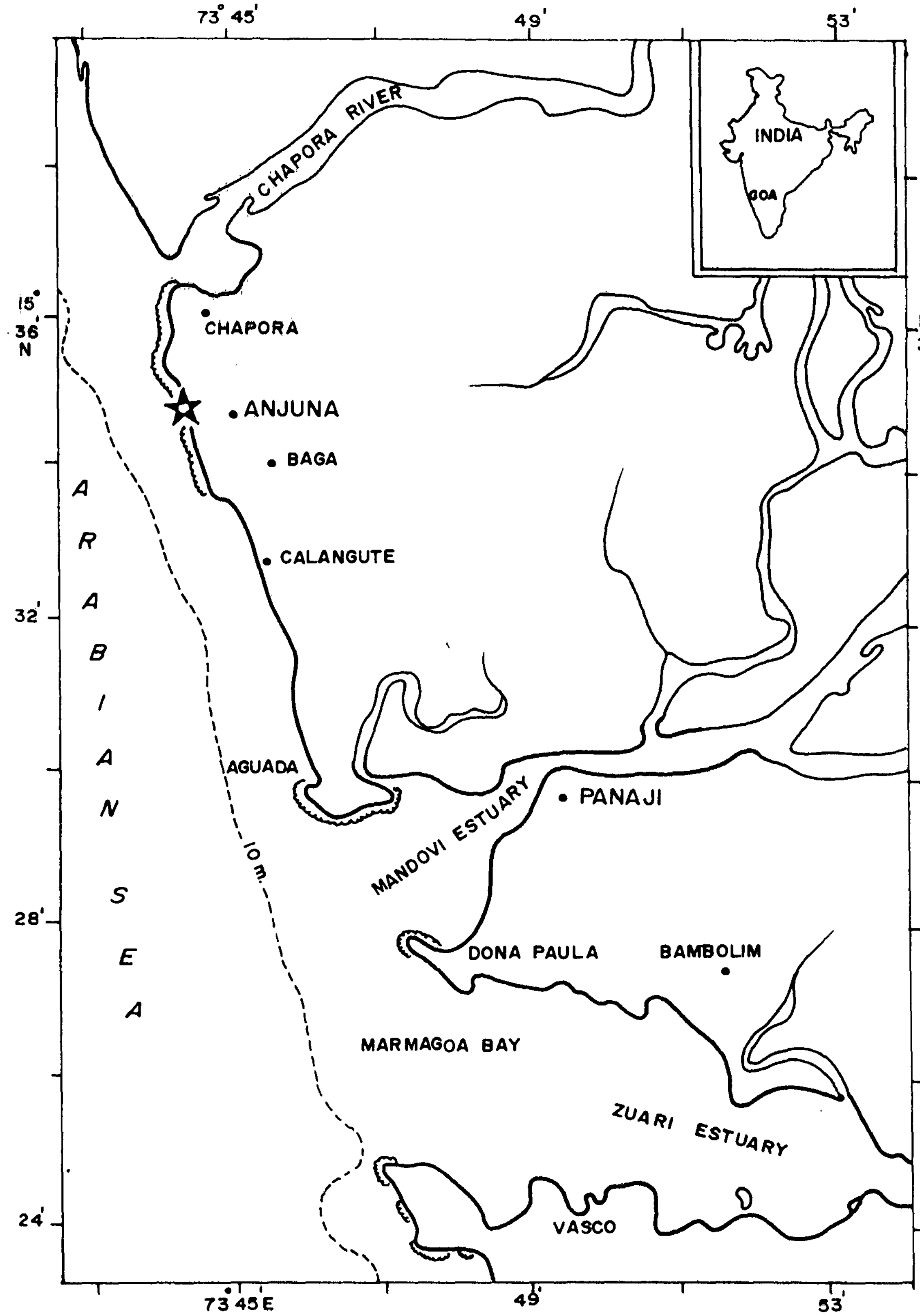


Fig. 1. Map of Goa coast showing the study area location. Anjuna.

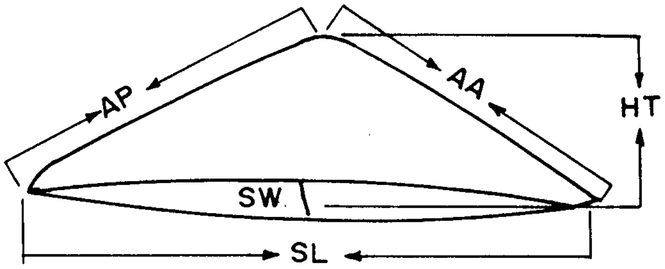
(1983) and is based on the principle that when sea water is titrated with silver nitrate the hallogen ions form a precipitate with silver. Chlorinity values thus obtained were converted into salinity in terms of parts per thousand using the following formula :

$$\text{Salinity} = 1.80655 \times \text{Chlorinity}$$

Dissolved oxygen in the sea water was analysed by the Winkler titration method described by Grasshoff *et al.* (1983). Water samples collected were fixed with Winkler A and B solutions in the field and analysed in the laboratory. The dissolved oxygen binds with manganese and liberates manganic ions when treated with an acid which further reacts with potassium iodide to liberate free iodine. This free iodine when titrated with thiosulphate gives the end point.

2.3 LABORATORY ANALYSES

About 15 limpets of various sizes were collected at quarterly intervals from December 1993 to September 1994 and maintained in aerated seawater tanks for three days. Observations revealed that the limpets completely voided their gut contents in three days. The different shell characteristics as shown in Fig. 2 *viz.* shell length, shell width, shell height, distance from apex to anterior end and distance from apex to posterior end were measured with a vernier callipers to an accuracy of 0.05 mm. The relationship between the different shell characteristics was determined by linear regression analysis.



ABBREVIATIONS

SL - SHELL LENGTH
HT - SHELL HEIGHT
SW - SHELL WIDTH
AA - DISTANCE FROM APEX TO ANTERIOR END
AP - DISTANCE FROM APEX TO POSTERIOR END

Fig. 2. General view of a limpet indicating the various shell measurements used in the present study (After Balamani. 1990).

Each limpet was then dissected in the laboratory while still in the shell so as to expose their gonad, and their sex determined. Males have creamish yellow gonads while females have greenish ovaries. The gonads were dissected from the body and the gonadal tissues and body tissues weighed separately to obtain the somatic and gonadal wet weights, whose sum yielded the total wet weight. The tissues were then dried in an oven at 60°C to constant weight to obtain somatic, gonadal and total dry weights. Weights were determined using a single pan Sartorius balance, to the nearest milligram.

The dried samples were powdered in a mortar and pestle and pressed into pellets using benzoic acid. Triplicates of each sample were analysed for their calorific content in a Parr adiabatic semi micro bomb calorimeter (model 1243).

The net temperature rise recorded for each sample was substituted in the following equation to obtain the heat of combustion:

$$Hg = (T \times W - (f + b))/m$$

where,

Hg = heat of combustion (cal/g)
T = net rise in temperature (°C)
W = energy equivalent of calorimeter (cal)
f = fuse wire correction (cal/cm)
b = benzoic acid correction (cal/g)
m = mass of the sample (g)

The energy equivalent of the calorimeter, W, was calculated from the following equation:

$$W = ((m_b \times 6318) + f)/T$$

where,

m_b = mass of benzoic acid (g) used to make pellets and 6318 is the value of energy released by 1g standard benzoic acid.

The benzoic acid correction is the mean value obtained by burning pellets of benzoic acid of 0.2g each and is equal to 6311 cal/g. The length of the wire taking part in the combustion is used to determine the fuse wire correction and since platinum wire was used, the correction is nil.

The relationship between the biomass of limpets in terms of wet weight, dry weight and energy values (cal) and shell length was determined by using log-log regression analysis.

2.3.1 ANALYSIS OF GUT CONTENTS

Limpets were collected from the study site during April 1994 and October 1994. These were dissected in the laboratory to expose their gut. The gut contents were collected and observed under a microscope. It consisted of algal materials in different stages of digestion. A haemocytometer (a glass slide with a cavity of 1 cm^2 subdivided into 100 squares of 1mm each) was used to estimate the percentage occurrence of each food item that could be identified.

2.3.2 MAINTENANCE OF LIMPETS IN THE LABORATORY

Throughout the period of study, some limpets were maintained in the laboratory in glass tanks containing aged sea water. Limpets of different sizes were collected from the area adjacent to the study site and kept in aerated sea water tanks. Rocks covered with algal mats were collected and placed in the tanks, serving as a source of food. The sea water and food were renewed every three days. Observations were made on the feeding and reproductive behaviour of the limpet. Attempts were also made to measure the amount of mucus secreted by the limpets. To determine the amount of mucus secreted, individual limpets were placed on glass panes and left in sea water tanks for 3 hours. After removing the limpets, a clean blade was run over the foot to collect the secreted mucus, which was then weighed.

2.4 MOVEMENT ANALYSIS

The movement pattern of the limpets were investigated in the field on two occasions by carrying out diurnal observations. It was observed that limpets moved only when covered by the tide.

An area situated 40m from the high tide line was chalked out for this. The position of each limpet was exacted by measuring its distance and angle from two reference points drawn with respect to the location of the sea.

The first set of observations were carried out on 25th-26th February 1995. The position of 80 limpets were marked and recorded during three consecutive low tides (12 hours intervals). The second set of observations were carried out from 15th to 18th May 1995. During this period the position of 24 limpets were marked and followed at every succeeding high tide.

2.5 POPULATION SIZE

The density of limpets in the study area was estimated every month from September 1993 to October 1994 using a 50cm x 50cm quadrat. Forty randomnly placed quadrats were enumerated. Limpets in cracks and fissures of the rock surface, but within the quadrat, were also included in the enumeration. Besides enumerating the limpets, the shell length of each individual limpet was recorded to indestructively estimate its biomass using regression equations mentioned earlier. The data was also used to obtain monthly shell length frequency distributions.

2.6 GROWTH

The growth of limpets was estimated by two methods. In the first method, the monthly shifts in modal peaks of the normal curves fitted to the size (shell length) frequency distribution were used to estimate the monthly growth rate. The second method involved the direct measurement of growth of tagged limpets in the field. The limpets were marked using tags. The tags (5mm x 5mm) consisted of a set of numbers printed on OHP film. The shell of the limpets were cleaned, wiped dry and tags were affixed using a glue. The limpets were marked at two places, on the anterior as well as the posterior side of the shell.

Various types of adhesives were experimented with, first in the laboratory and later in the field during 1992-93 to select a suitable glue. Initial trials were made using Quickfix. Within a period of three months no marked limpet could be recovered. Trials were also made using dental cement. This too, gave similar results and moreover, the powder was difficult to handle on the shore. Attempts were made using a third glue (Supercement - a cyanoacrylic glue). Results were better than the previous glues but was still inadequate for long term marking. The glue finally selected was an epoxy resin (Araldite Rapid, Ciba-Geigy). This glue was very efficient and tags remained for more than one year.

Limpets were tagged using Araldite during September 1993 to October 1994, to study its growth and monitor their fate. The shell length of the marked limpets were measured whenever they were recovered during the subsequent field visits using a vernier callipers to an accuracy of 0.05 mm. A total of 947 limpets were marked during this period. During the course of observations, it was noted that some of the tags were getting eroded due to environmental conditions. These limpets were retagged.

The growth data so obtained was checked to see whether it followed the von Bertalanffy growth model given by the following equation:

$$L_t = L_\infty (1 - e^{-K(t - t_0)})$$

where, L_t = age at length t
t_0 = theoretical age at which L = 0
L_∞ = asymptotic length
K = growth constant

The growth parameters *viz.* L_∞ and K were estimated using Munro's equation (1982):

$$\ln (L_\infty - L_1) - \ln (L_\infty - L_2) = K (t_2 - t_1)$$

A trial value of L_∞ was assigned in the above equation using the data obtained from tagging, and K values along with its coefficient of variation (C.V.) computed.

$$\text{C.V. of } K = \sigma \text{ of } K \text{ values / mean value of } K$$

The C.V. was calculated for different trial values of L_∞ and the trial value which resulted in the lowest C.V. was selected as the estimate of L_∞. This method provides accurate estimates, irrespective of the the length of the time intervals.

Seasonal growth was estimated by the forced Gulland and Holt plot (1959) where K was given by

$$K = \bar{Y} / L_\infty - \bar{X}$$

where, $\bar{Y}$ = mean growth rate per month

$\bar{X}$ = mean shell length

2.7 MEASUREMENT OF PRODUCTION

Production of the population of *C. radiata* at Anjuna was calculated using the method outlined by Crisp (1984). A monthly frequency size (shell length) distribution table, with intervals of 10mm, was constructed using the shell length data of limpets obtained during the monthly density measurements. In this method, production sums up for all age groups and is given by:

$$\text{Production} = \sum_{t=0}^{t=1} \sum_{0}^{n} f_i \cdot G_i \cdot \bar{w}_i \blacktriangle t$$

where,

G_i is the specific growth rate of size group *i*

$\overline{w}_i$ is the mean weight of size group i

f_i is the number of the individuals of size group i

Δt is the time interval

The total standing stock biomass of size class i is thus denoted as:

$$f_i \times \overline{w}_i$$

The specific growth rate, G_i, was calculated using the following equation:

$$G_i = b \cdot K \cdot (L_\infty - L_i)/L_i$$

where b is the exponent of the length - weight relation.

The biomass of limpets of size group *i* was estimated using the log-log regression equations obtained in the quarterly biomass-shell length analyses. Production of different tissue components *viz.* total, somatic, gonadal and gamete were estimated. As gonadal biomass/energy was not significantly correlated with shell length, it was estimated from the difference between the total and somatic biomass/energy.

Gamete production was estimated indirectly. The gonad index in terms of dry weight was first calculated by expressing the gonad dry weight as a percentage of the total dry weight. Males and females limpets having a dry index above 25% were assumed to represent limpets which had not yet spawned *i.e.* had not released gametes. A log-log regression analysis of gonadal biomass in terms of wet weight, dry weight and calories and shell length was then performed to estimate the parameters of the power curve. The non-linear regression equation obtained was statistically significant ($r = 0.91$, $P < 0.001$). Using this equation, the expected gonad biomass in terms of wet weight, dry weight and calories were calculated for the limpets recorded in the monthly density measurements. The observed gonad biomass were calculated using the difference of total and somatic biomass-shell length relationship obtained in the quarterly analyses. The difference between the expected and observed values gave an estimate of the biomass of gametes spawned.

Estimates of monthly, seasonal, and annual production were obtained. The 95% confidence limits of production were calculated from the 95% confidence limits of biomass values.

2.8 RESPIRATION

Aged and filtered sea water was used for the respiration experiments. Experiments were carried out at three different temperatures *viz.* 23°C, 28°C, and 35°C in the laboratory using a temperature controlled room for lower temperature and a thermostatically controlled water bath for higher temperature. Limpets of different sizes were gradually acclimatized to the change in temperature prior to the experiments. The experiments were carried out for two hours with different sets of limpets placed in jars filled with sea water, each set comprising of three limpets of similar size and weight. The dissolved oxygen content of the sea water in the jars were determined prior to the experiment. Every experimental jar had an accompanying control. At the end of two hours the water in the jars were once again analysed for dissolved oxygen. Dissolved oxygen was analysed by the Winkler titration method (Grasshoff *et al.*, 1983). The difference between the control and experimental jars represented the amount of oxygen utilised by the limpets.

Respiration rate (R) was calculated using the equation described by Omori and Ikeda (1976) which is given by:

$$R = ((C_{OX} - E_{OX}) \times 1000 \times V) / t \times N$$

where,

R = respiration rate (ml O_2/animal/hr)
C_{OX} = Dissolved oxygen in control jar (ml O_2/hr)
E_{OX} = Dissolved oxygen in experimental jar (ml O_2/hr)
V = volume of experimental jar (l)
t = incubation time (hrs)
N = number of animals

At the end of the experiments the soft tissue of the limpet was separated from the shell and its wet weight obtained. The same was dried in an oven at 60°C to obtain dry weight. The dry weights (W) and the respiratory rate (Q) in calories (obtained by multiplying the respiratory rates by the oxy-calorific coefficient 4.83) was calculated. When Q is plotted against the logarithm of weight (w), a linear relation described by the following equation is obtained:

$$Q = A \times w^{b}$$

The value of the constant A is dependent on temperature but not the exponent 'b'. The relation between $\log_{10}$ of A and temperature is linear and through regression analysis, A at different temperatures can be evaluated.

Energy losses through respiration of the population of *C. radiata* at Anjuna was calculated by the method outlined by Crisp (1984). The size frequency table at 10mm intervals was constructed as described for the estimation of production. The respiration rates of the limpets at the mean temperatures recorded in the field were estimated from the laboratory experiments. Annual energy losses by respiration is given by:

$$R = \sum_{o}^{m} A_{j} \cdot \blacktriangle t_{j} \cdot \left(\sum_{o}^{n} f_{i} \cdot \overline{w}_{i}^{b} \right)$$

where,

A_j is the value of A at mean temperature during the period

$\blacktriangle t_j$ is the period of interval in hours

f_i is the number of limpets of size class i

$\overline{w}_i$ is the mean weight of size class i

Biomass of size class *i* was estimated using the quarterly log-log regression equations. The 95% confidence limits of respiration losses were calculated from the 95% confidence limits of biomass.

2.9 STATISTICAL ANALYSES

All statistical analyses were adopted from Sokal and Rohlf (1981).

2.9.1 ANALYSIS OF POLYMODAL FREQUENCY DISTRIBUTIONS

The polymodal frequency distribution of the monthly shell length data was separated into component Gaussian curves with unequal variances by statistically fitting the curves and testing the goodness of fit using chi-square test. The procedure of fitting normal curves with unequal variances involved the following steps. The size data (shell length) of individual limpets were sorted in ascending order and a frequency table at 1mm class intervals constructed. The number of curves to be fitted was determined by the number of modal peaks. The size data was then divided into the number of groups (curves) required and the means and variances of each group determined separately.

$$\sigma_i^2 = ((x_i - \mu_i) / N_i)^2$$

where.

σ_i^2 = variance of group i

x_i = size data in group i

μ_i = mean of group i

N_i = number of values in group i

The data (shell length) was allocated into the groups by determining the probability of their falling under each of the normal curves and reallocate to the group with the highest probability. The means and variances and number of data in each group were then recalculated. Iterations were continued until the probabilities were maximized. The normal probability density function is represented by the following expression:

$$f(x, \mu_i, \sigma_i) = (1/\sqrt{2\pi}) \times (1/\sigma_i) \times e^{-\frac{1}{2}(((x_i - \mu_i)/\sigma_i))^2}$$

After estimating the parameters, the function was evaluated for each curve to obtain the expected frequencies at 1mm size class intervals. Simpson's one third rule was used to integrate the area under the normal curve. The goodness of fit of the curves was tested using the chi-square statistic:

$$\text{chi-square} = \frac{(\text{Observed frequency} - \text{Expected Frequency})^2}{\text{Expected frequency}}$$

The level of significance of the fit was determined by comparing the calculated chi-square value with the tabulated value of chi-square at N-E-1 degrees of freedom where N denotes the number of class intervals and E is the number of estimated parameters.

2.9.2 STANDARD DEVIATION

The standard deviation of the mean (σ) was calculated the following way

$$\sigma = \sqrt{\Sigma\ (X-\overline{X})^2/(n-1)}$$

where.

$\overline{X}$ = mean of the sample

n = sample size

2.9.3 STANDARD ERROR

Standard error of the mean at 95% confidence limits was calculated using the formula

$$\overline{X} \pm 1.96 \cdot \sigma/\sqrt{n}$$

where.

$\overline{X}$ = mean of the samples

σ = standard deviation

n = sample size

2.9.4 CORRELATION ANALYSES

The Karl Pearson correlation coefficient (r) between two variables was calculated between shell length and other shell parameters, shell length and other tissue parameters and the levels of significance determined at n-2 degrees of freedom where N is the number of paired observations using the following formula:

$$r = N \cdot \Sigma XY - ((\Sigma X)\ (\Sigma Y)) / \sqrt{([N\ \Sigma X^2 - (\Sigma X)^2\ ] - [N\Sigma Y^2 - (\Sigma Y)^2])}$$

where.

N = sample size

X = independent variable

Y = dependent variable

2.9.5 REGRESSION ANALYSES

Regression analyses were carried out between variables with a significant correlation coefficient. Two types of regressions were carried out

(1) Linear regression

(2) Log - log regression

(1) Linear regression

A linear regression was carried between various shell characteristics of the limpets. The regression equation of Y on X was used.

$$b_{yx} = (\Sigma XY - ((\Sigma X * \Sigma Y) / N)) / (\Sigma X^2, - ((\Sigma X)^2 / N))$$

$$a_{yx} = \overline{Y} - b_{yx} \cdot \overline{X}$$

where.

b_{yx} and a_{yx} are the slope and intercept respectively

X = independent variable

Y = dependent variable

(2) Log - log regression

It is represented by the power equation

$$Y = a * X^b$$

where.

X = independent variable

Y = dependent variable

a and b are constants.

Log - log regression was carried out between shell length and the different tissue parameters.

To fit the regression curve linear regression analyses was carried out using logarithmically transformed X and Y variables. The resulting equation thus is

$$\text{Log } Y = b \text{ Log } X + \text{Log } a$$

The slope of the equation is an estimate of b of the power function while the antilog of the constant gives an estimate of a.

The standard error, significance tests and 95% confidence limits of regression statistics were computed as outlined in Sokal and Rohlf (1981).

2.9.6 STUDENT'S *t* TEST

A Student's *t* test was performed to test whether the difference between the mean values of male and female limpets were statistically significant. The *t* value was calculated using the following formula:

$$t = (\overline{X}_1 - \overline{X}_2) / S.E.$$

where.

$\overline{X}_1$ = mean of sample 1

$\overline{X}_2$ = mean of sample 2

standard error (S.E.) = $\sqrt{((\sigma^2{}_1 / N_1) - (\sigma^2{}_2 / N_2))}$

where.

$\sigma^2{}_1$ = variance of sample 1

$\sigma^2{}_2$ = variance of sample 2

N_1 = number of individuals in sample 1

N_2 = number of individuals in sample 2

CHAPTER III

ECO-BIOLOGY OF *CELLANA RADIATA*

3.1 STUDY AREA

The area selected for the study at Anjuna (Fig. 3), is a rocky body, with high cliffs projecting out towards the shore. This structure is a long stretch projecting perpendicularly into the sea upto around 60m, most of which is exposed during an average low tide (Plate I-a). The substratum is mainly metagreywacke upto 40m with laterite boulders beyond it. The area, with its elevations, depressions, crevices and tidepools, harbours diverse flora and fauna. The maximum elevation from the low tide to the high tide is about 4m (Peter, 1989). The tidal amplitude along the coast is around 2.5m. Tidal levels at Marmagoa port, denoted as heights above Chart Datum, are presented in Table 1.

Like most other rocky shores, zonation is discernible at Anjuna too. The shore can be classified into an upper littorinid zone, a middle barnacle-oyster zone, and a lower tubiculous polychaete zone (Peter, 1989). A large number of algal species can also be observed on the shore, the distribution of which has been described by Acharya (1989). The upper littoral zone is dominated by green algae *viz. Enteromorpha* spp., *Ulva* spp., and *Chaetomorpha* sp. with sparse growth in the first twenty meters. The mid littoral region is colonised by algae such as *Enteromorpha* spp., *Ulva* spp. and *Chaetomorpha* sp. belonging to

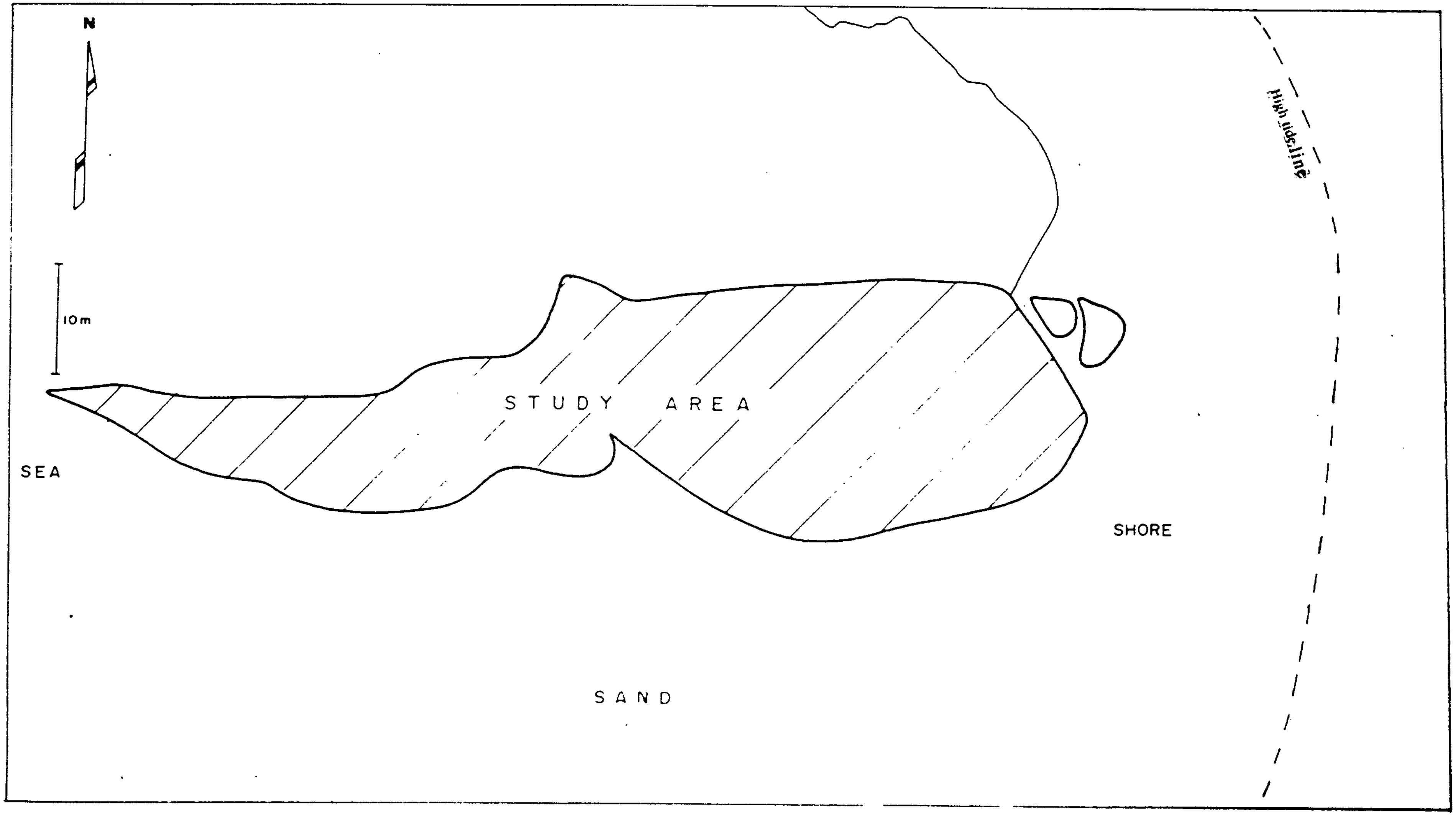
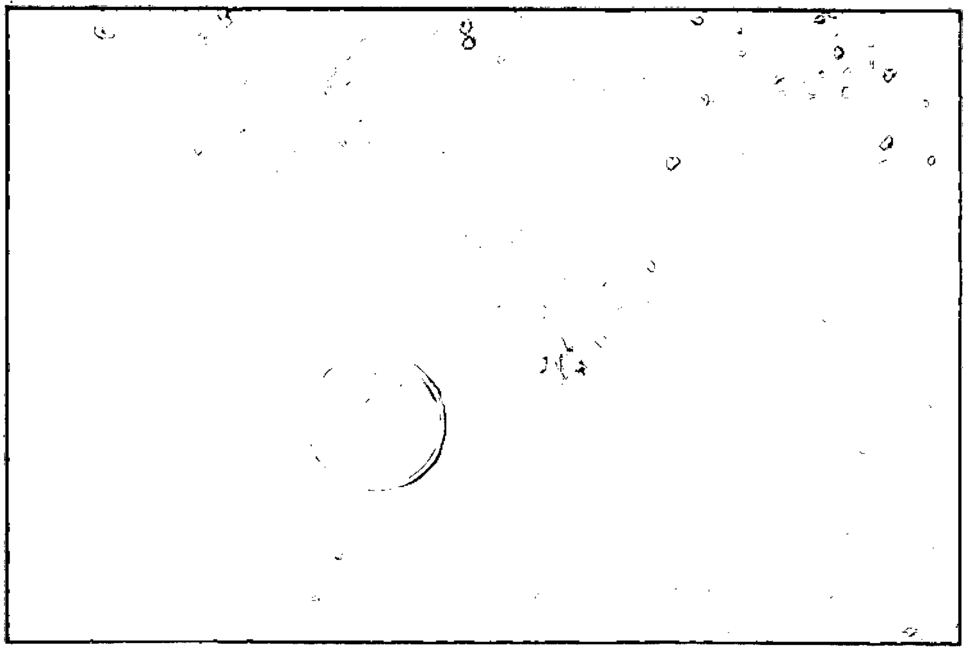


Fig. 3. The study area at Anjuna (After Peter. 1989).

PLATE I

a. The general view of the study area at Anjuna.



b. The limpet *Cellana radiata* inhabiting the rocky shore.

TABLE 1

Tidal levels at Mormugao port.

Tide level	Height (m)
Lower low water (spring)	0.00
Mean lower low water	+0.37
Mean higher low water	+1.05
Mean sea level	+1.30
Mean lower high water	+1.78
Mean higher high water	+2.06
Higher high water (spring)	+2.30

Chlorophyta: *Padina* sp. and *Sargassum* sp. belonging to Phaeophyta:, and *Gracillaria* sp., *Hypnea* sp. and *Centroceras* sp. of Rhodophyta. The lower littoral region is dominated by rhodophytes *e.g. Gracillaria* sp., *Hypnea* sp., *Centroceras* sp., *Ceramium* sp., *Polysiphonia* sp. and *Gelidium* sp..

3.2 ENVIRONMENTAL PARAMETERS

The four environmental parameters *viz.* air temperature, sea surf temperature, salinity and dissolved oxygen recorded every month at the study site are graphically depicted in Fig. 4. The lowest air temperature (28°C) and sea temperature (27.8°C) were recorded in the month of July. During the month of November, the highest air temperature (32.4°C) and sea temperature (31.9°C) were recorded.

Air and surf water temperature values followed similar trends. Air temperature values were within the range as recorded at the Indian Meteorological Department (IMD), Panaji. Other climatic factors such as the maximum and minimum mean monthly temperatures, rainfall and relative humidity are presented in Table 2. The average annual rainfall is 2760mm which is largely due to the southwest monsoons lashing during June-August (IMD, Panaji). Based on climatic factors, the year can be roughly divided into three seasons: pre-monsoon season (February-May), monsoon season (June-September) and the post-monsoon season (October-January).

Salinity values ranged from 15.12‰ in August to 35.63‰ in

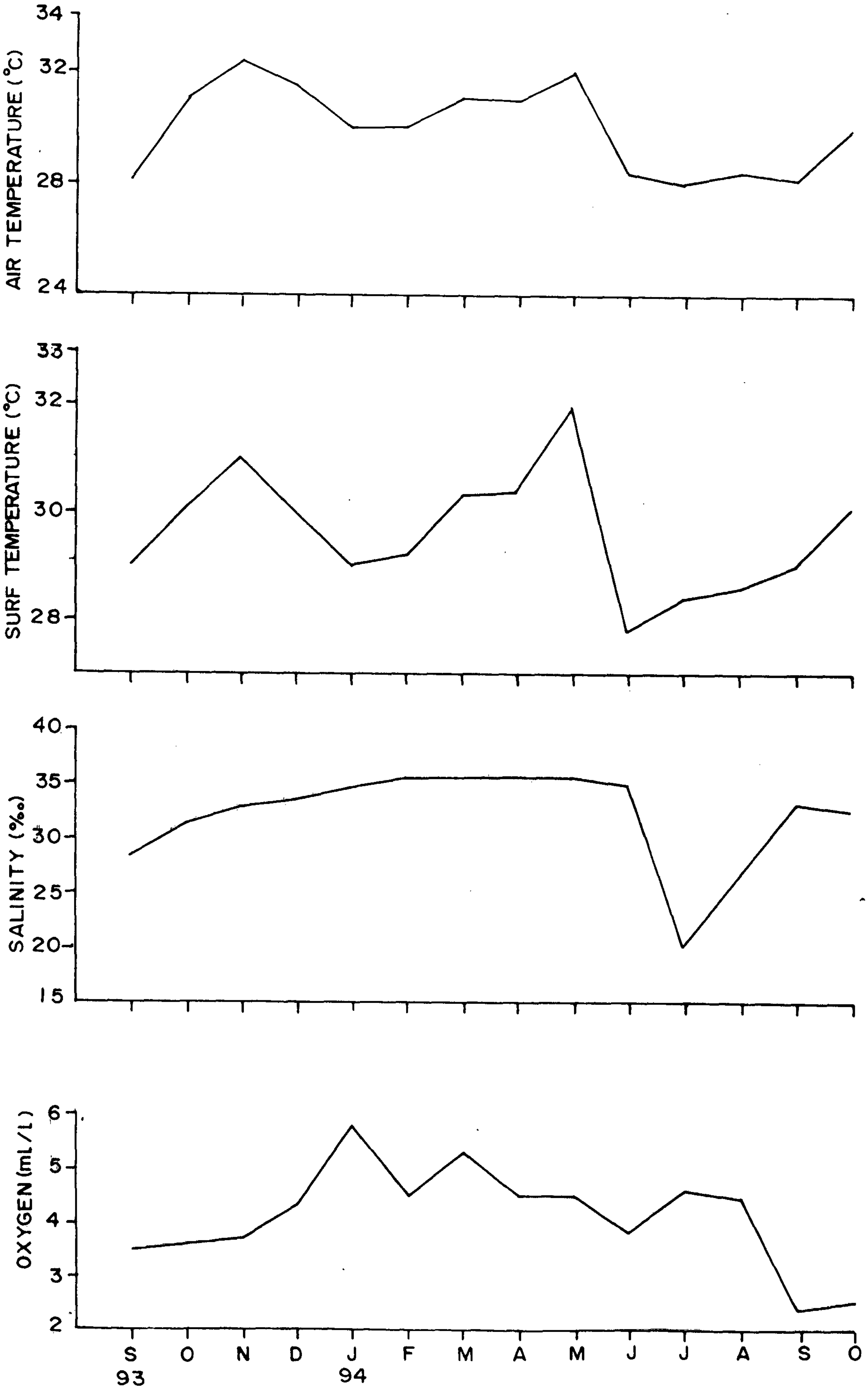


Fig. 4. Monthly variation in air temperature, surf temperature, salinity and dissolved oxygen recorded at Anjuna.

TABLE 2

Environmental parameters recorded at IMD. Panaji.

MONTHS	MEAN MAX. (°C)	MEAN MIN. (°C)	RAINFALL (mm)	RELATIVE HUMIDITY (%)
SEPTEMBER'93	29.3	23.8	210.5	93.5
OCTOBER	31.3	24.0	168.9	93.0
NOVEMBER	33.6	23.3	2.0	80.0
DECEMBER	32.3	21.3	9.8	79.5
JANUARY'94	32.5	20.9	0.0	79.5
FEBRUARY	31.4	20.8	0.0	79.5
MARCH	32.3	24.9	0.0	84.0
APRIL	33.1	25.4	18.7	82.0
MAY	33.4	26.7	31.6	79.5
JUNE	29.6	25.1	767.8	87.5
JULY	28.6	24.1	896.5	91.5
AUGUST	29.0	24.3	666.9	91.5
SEPTEMBER	29.9	23.4	228.7	90.5
OCTOBER	31.6	23.8	283.0	91.5

May. The decline in salinity followed the onset of the monsoons. Analyses of water samples suggested a decrease in dissolved oxygen content during the month of June (3.8ml/l) while highest values were recorded in January (5.8ml/l).

3.3 LIMPETS OF ANJUNA

Patellid limpets are molluscs of littoral and shallow water occurence and are widely distributed (Fig. 5). Only one species of limpets, *Cellana radiata* (Born, 1778), was recorded in the study area (Plate I-b) and its taxonomic position is as follows:

Class: Gastropoda Cuvier, 1797
    Subclass: Prosobranchia Milne-Edwards, 1848 -
        Order: Archaeogastropoda Thiele, 1925
            Family: Patellidae Rafinesque, 1815

Three genera are placed in the family Patellidae, discernible on the basis of the gill cordon and epipodial fringe. They are *Patella*, *Cellana* and *Nacella*. In the genus *Cellana*, the gill cordon is interrupted by the head and the epipodial fringe is absent.

The dorsal and ventral view of *C. radiata* is shown in Fig. 6. The shell of *Cellana radiata* is of moderate size upto around 37mm in length, rather lightly built, roundly ovate and with a subcentral nucleus. Sculpture consists of numerous regularly

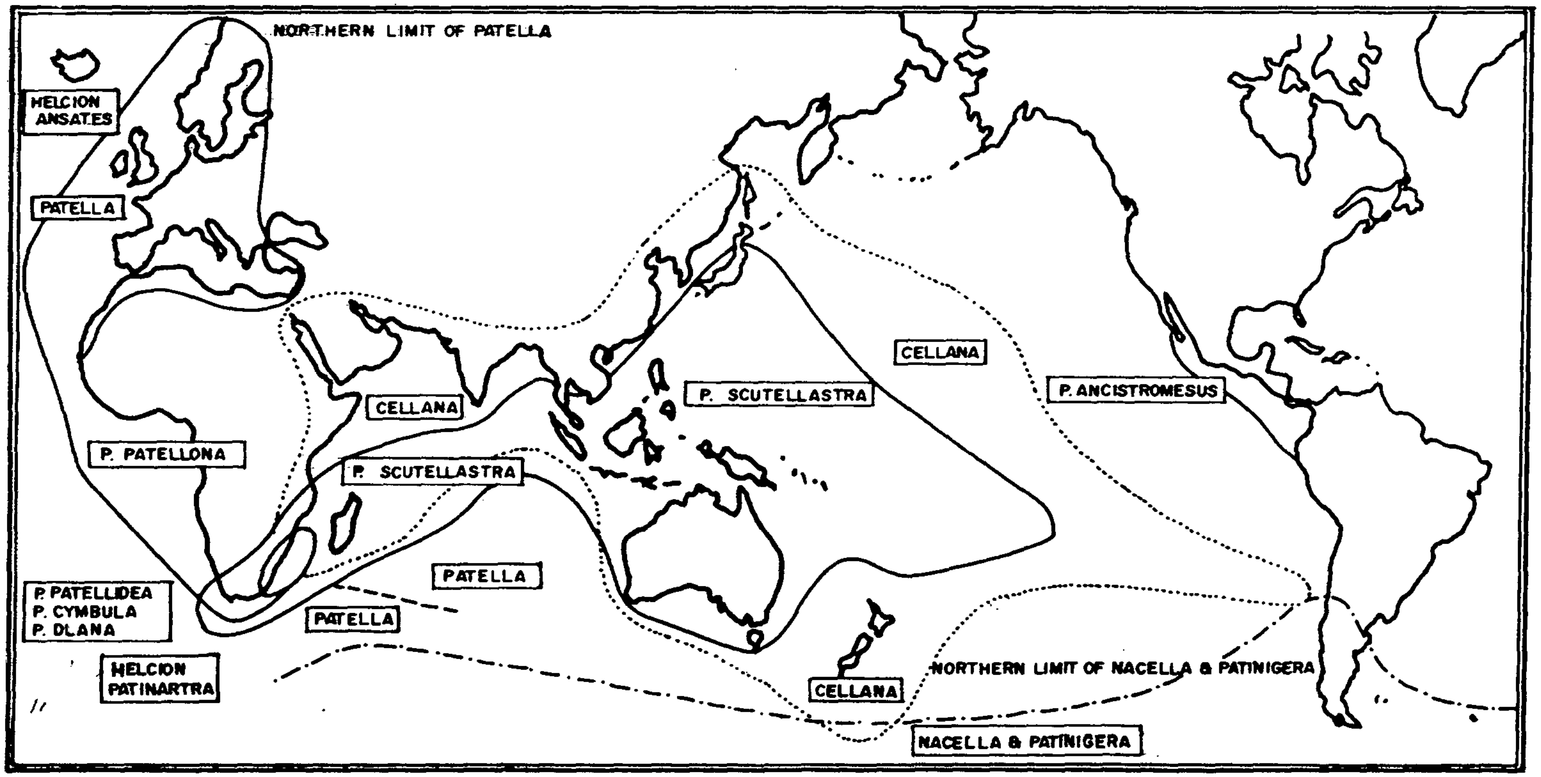


Fig. 5. Geographical distribution of the family Patellidae, (after Powell, 1973).

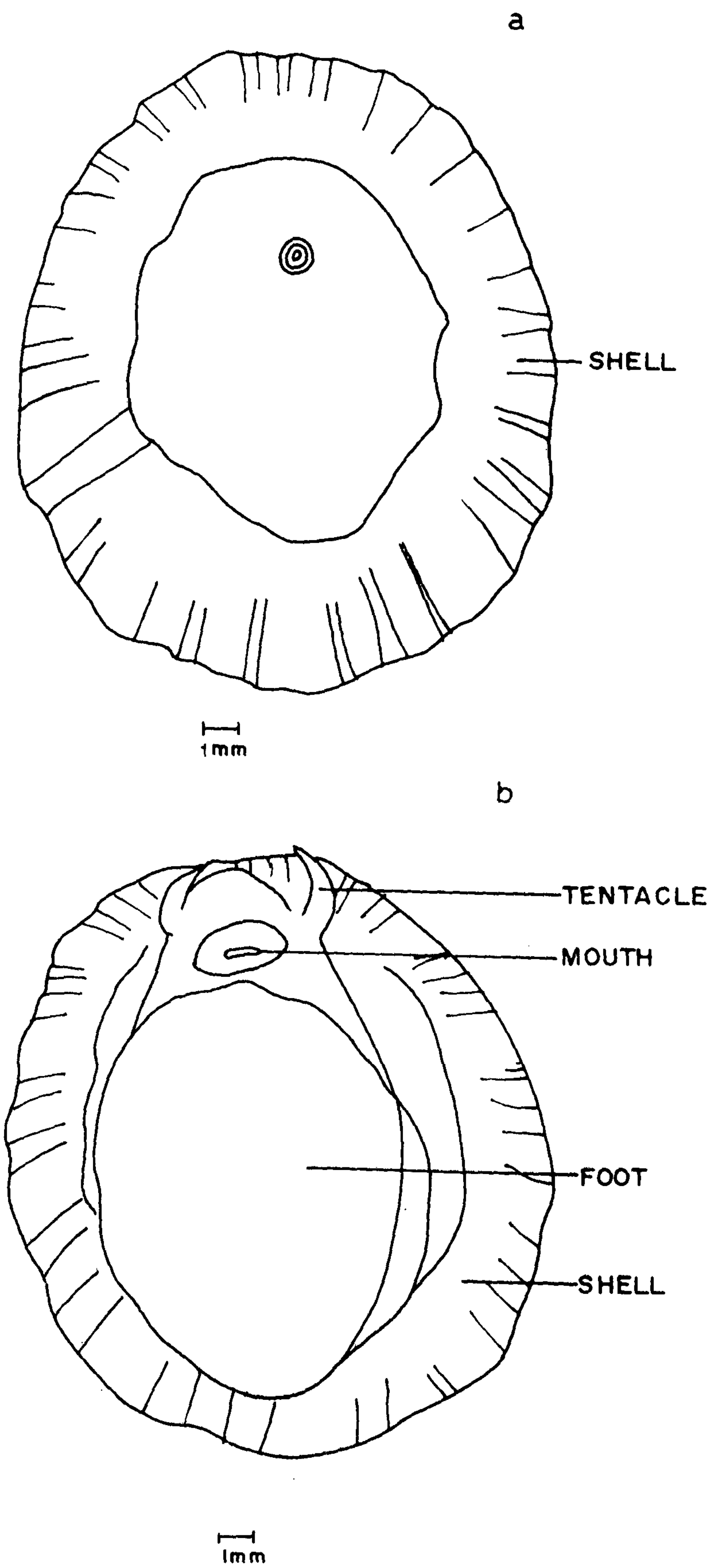


Fig. 6. The dorsal (a) and ventral view (b) of *C. radiata* (After Balamani, 1990).

flat topped radial riblets separated by linear grooves. There are around 9-11 bifid radial streaks in rather greyish or purple, upon a yellowish ground. The spatula is chestnut brown but most of it is clouded with a whitish callus.

3.4 ALLOMETRIC RELATIONSHIPS

The linear regression analyses carried out to determine the relationship between shell length and other shell parameters *viz.* shell width, distance from apex to anterior end, distance from apex to posterior end and shell height, with their 95% confidence limits, are graphically presented in Fig. 7 to Fig. 14. The standard error of the estimates are given in Table 3. Slight variations in the estimates are observed for the different months. The results of these analyses are useful for estimating other shell size parameters from shell length data. This is particularly useful for estimating shell sizes of limpets located in areas which are not easily accessible for recording measurements.

The relationship between size and biomass is best expressed by the power function equation. Results of the regression analyses for the power curve fit between shell length and total wet weight, total dry weight, total calories, somatic wet weight,somatic dry weight and somatic calories for the different months are illustrated in Fig. 15 to 26. The standard error of the estimates are presented in Table 4. It can be seen that

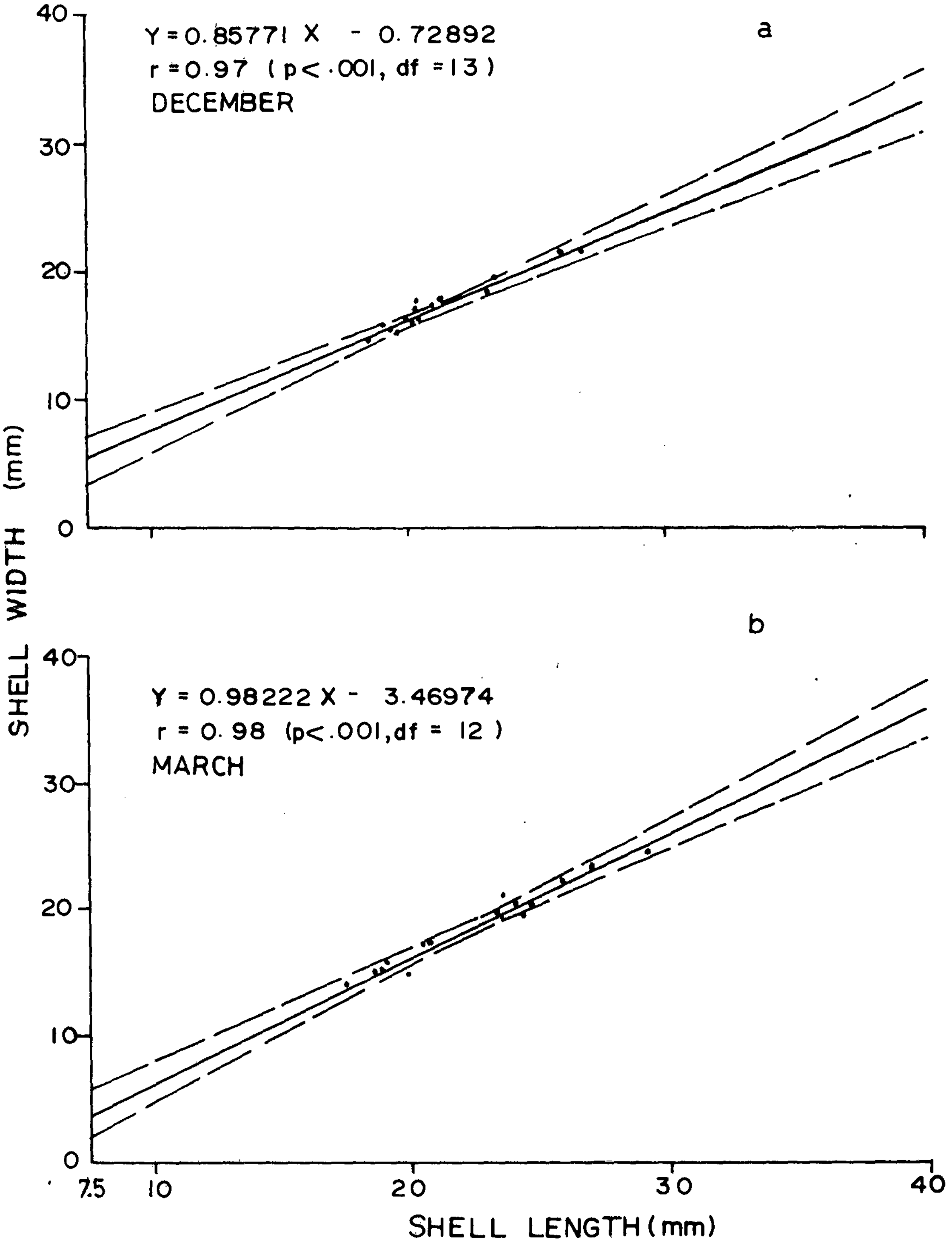


Fig. 7. The relationship between shell length and shell width for December (a) and March (b).

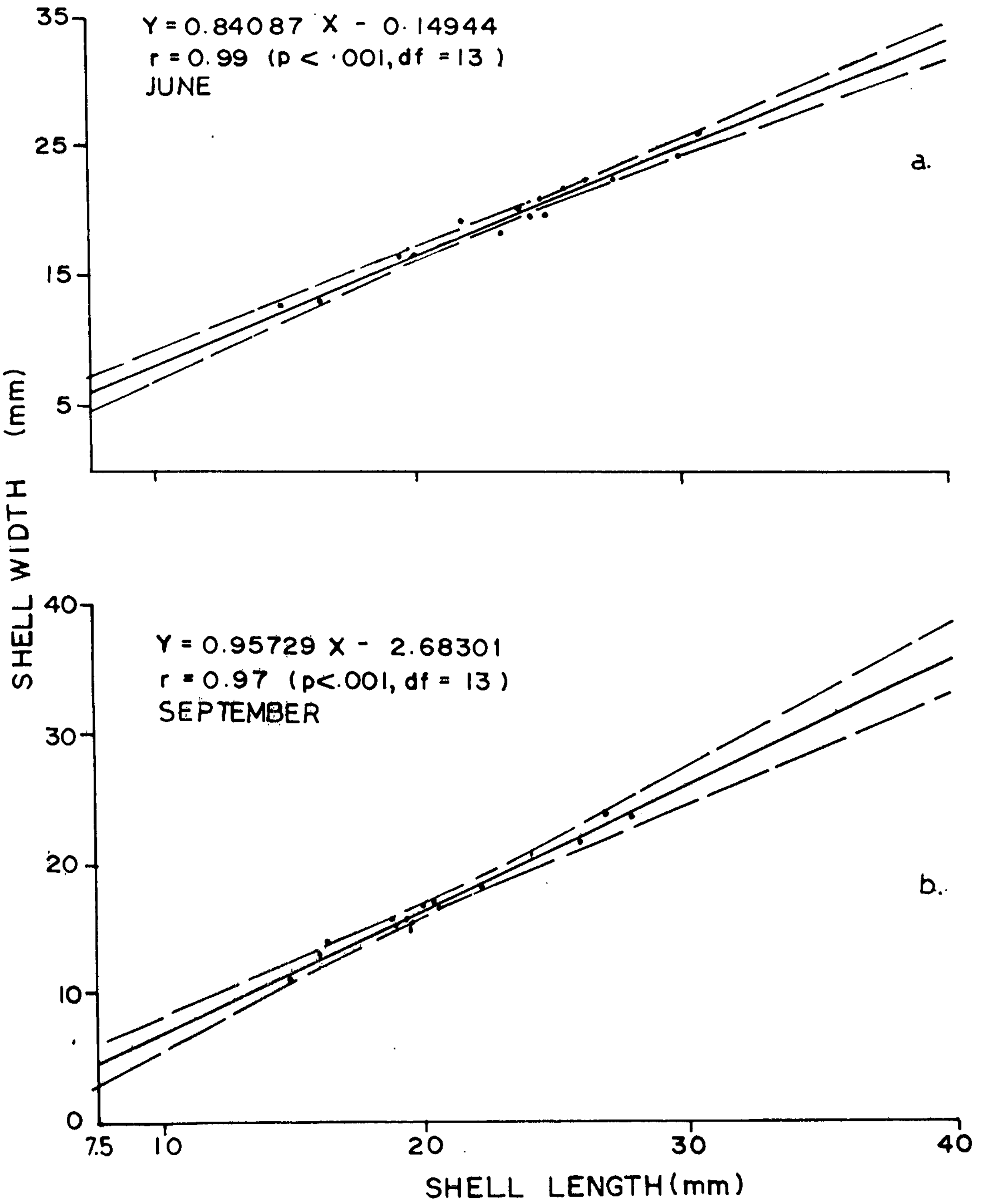


Fig. 8. The relationship between shell length and shell width for June (a) and September (b).

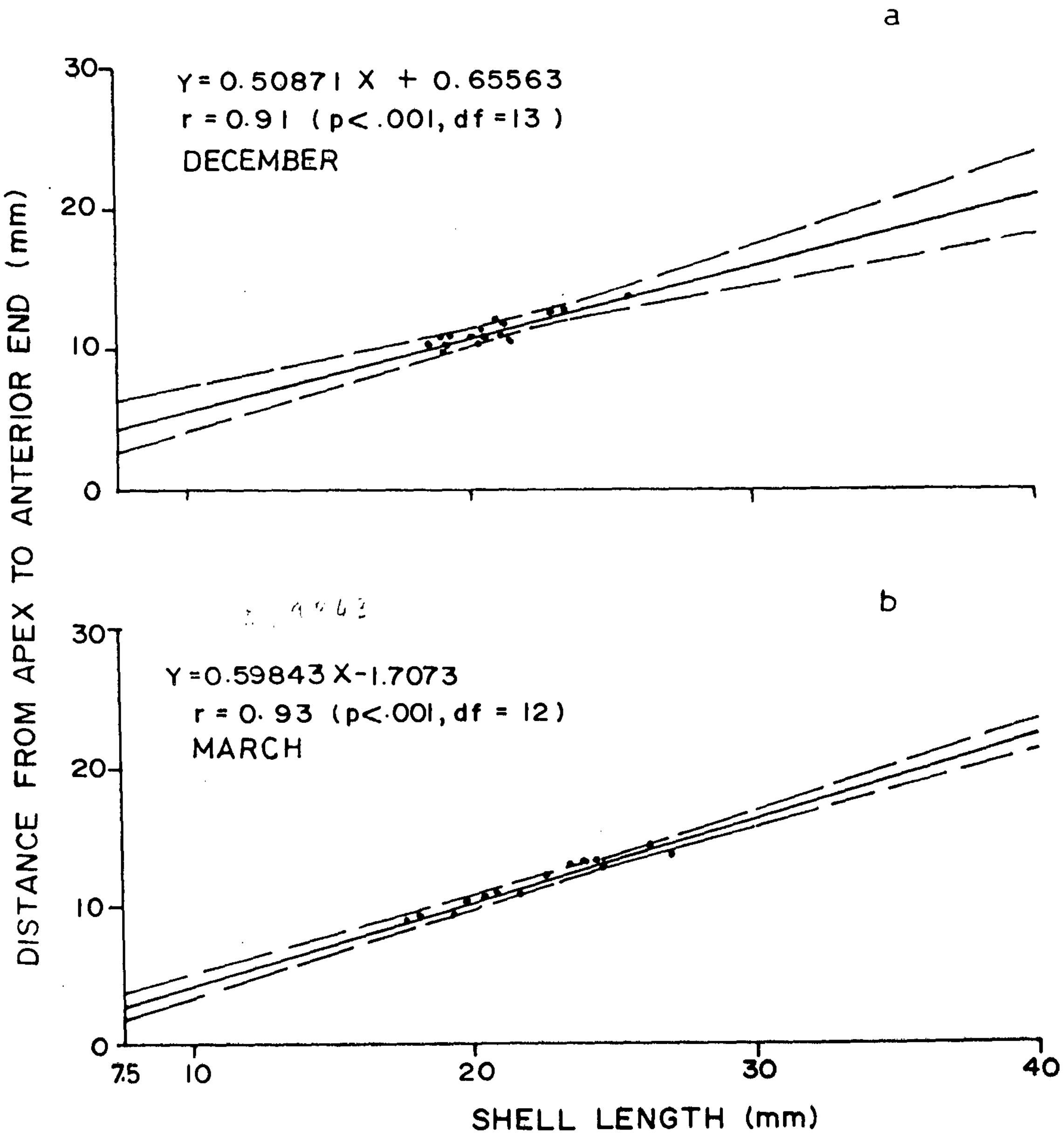


Fig. 9. The relationship between shell length and distance from apex to anterior end for December (a) and March (b).

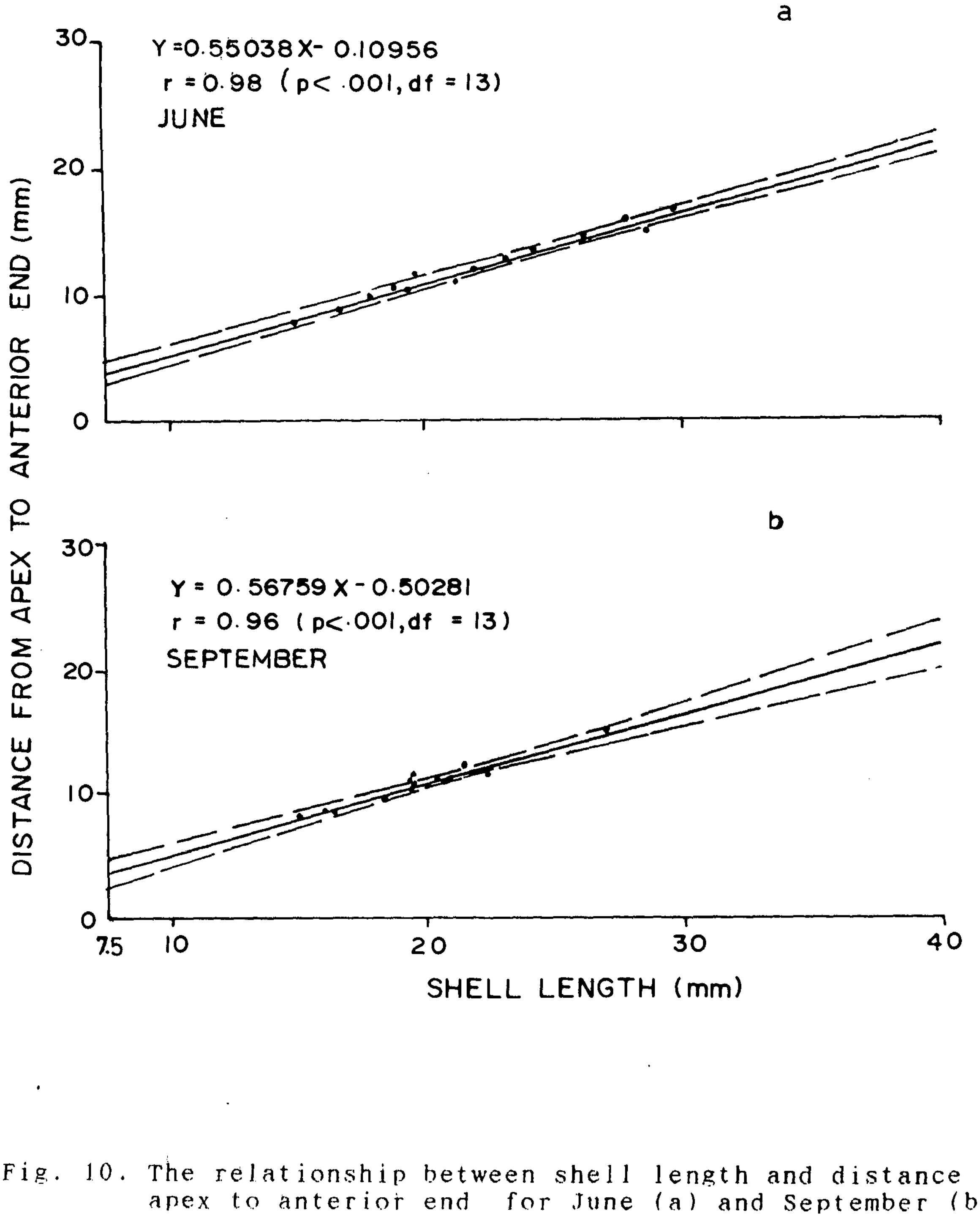


Fig. 10. The relationship between shell length and distance from apex to anterior end for June (a) and September (b).

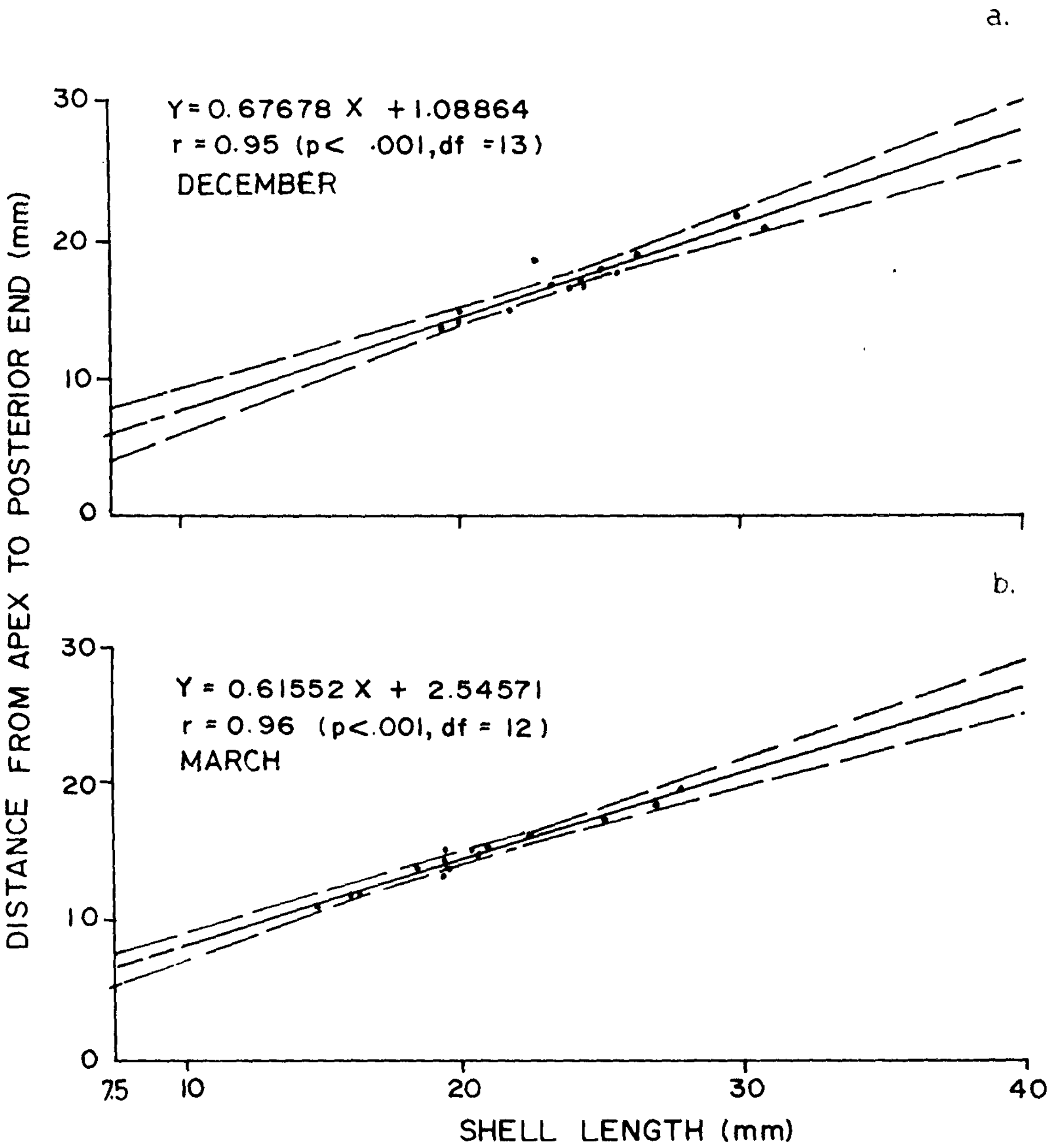


Fig. 11. The relationship between shell length and distance from apex to posterior end for December (a) and March (b).

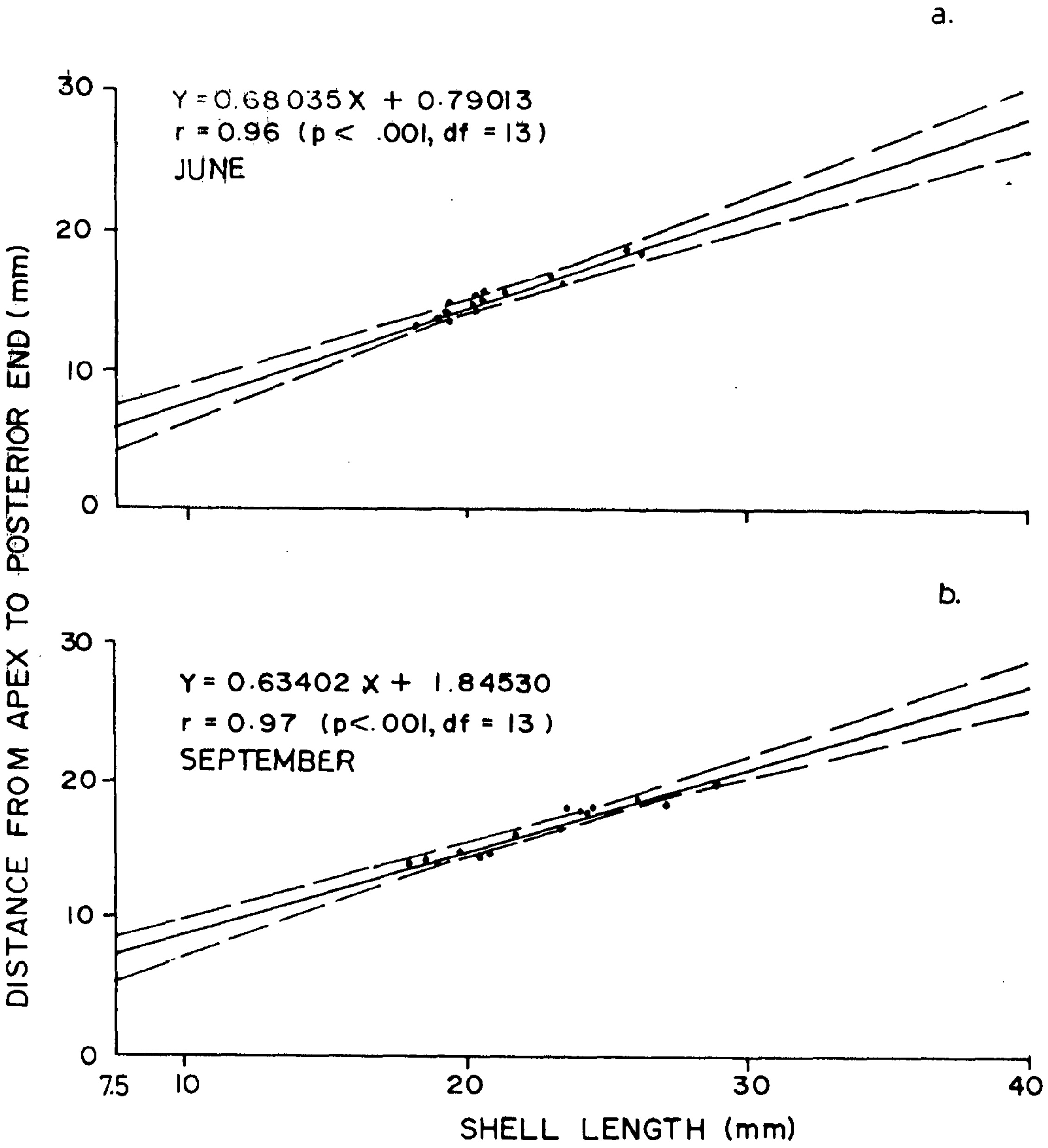


Fig. 12. The relationship between shell length and distance from apex to posterior end for June (a) and September (b).

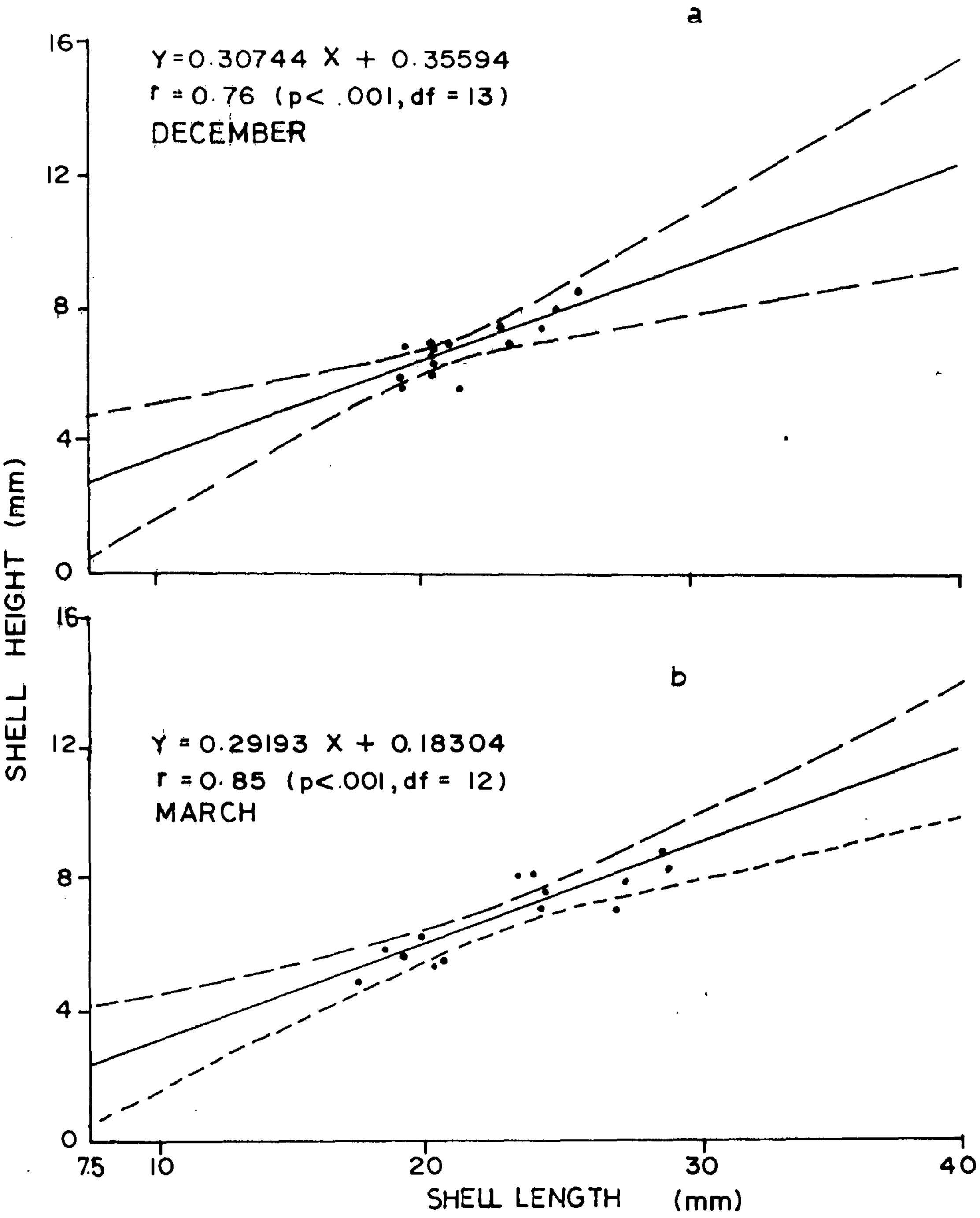


Fig. 13. The relationship between shell length and shell height for December (a) and March (b).

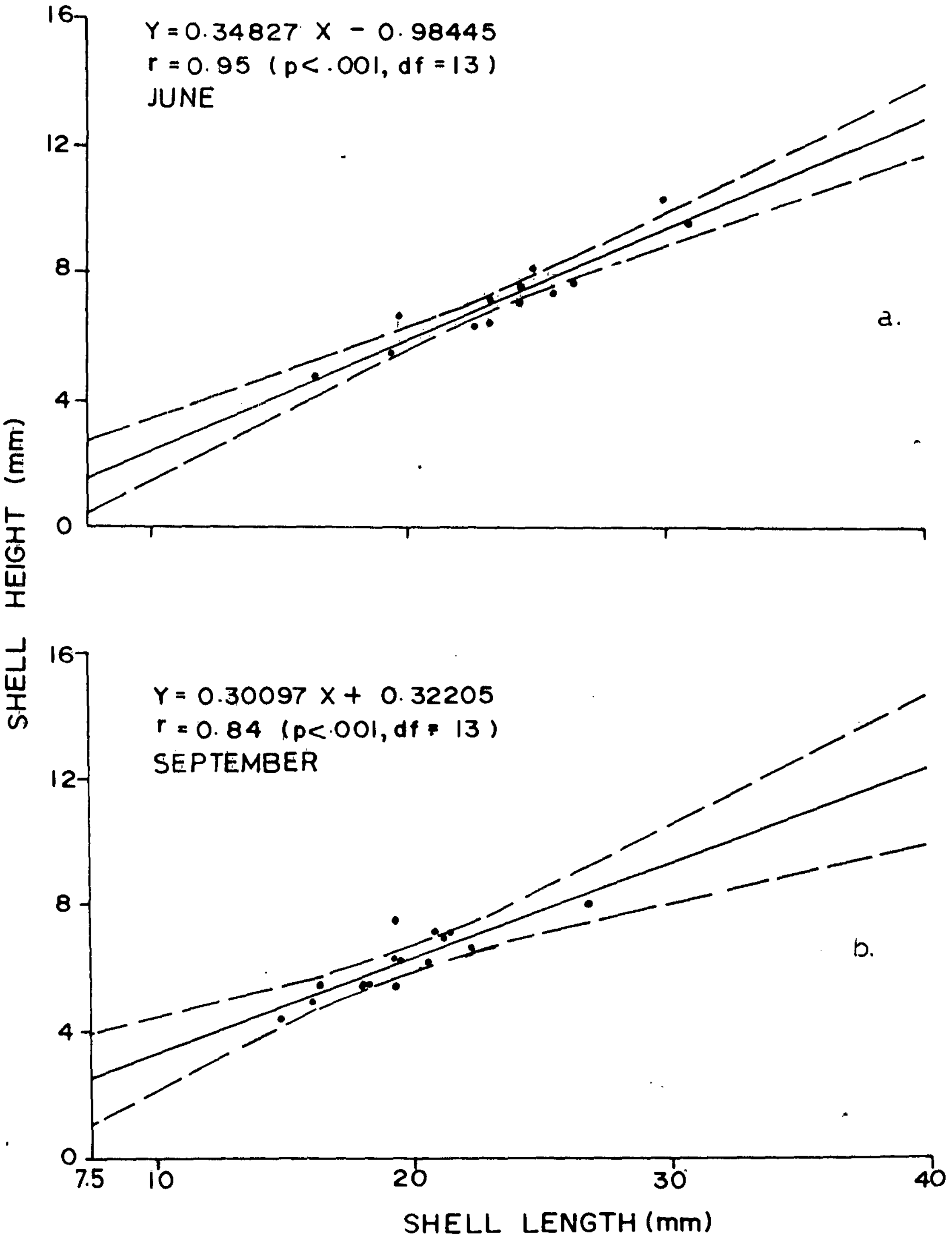


Fig. 14. The relationship between shell length and shell height for June (a) and September (b).

TABLE 3

Results of the linear regression analysis (± S.E.) carried out between shell length and various shell parameters

PARAMETER	MONTH	r	m ± S.E
SW	DECEMBER	0.97***	0.85771 ± 0.05657
	MARCH	0.98***	0.98222 ± 0.05840
	JUNE	0.99***	0.84087 ± 0.03790
	SEPTEMBER	0.97***	0.95729 ± 0.06117
AA	DECEMBER	0.91***	0.50871 ± 0.06574
	MARCH	0.98***	0.59843 ± 0.02987
	JUNE	0.98***	0.55038 ± 0.02632
	SEPTEMBER	0.96***	0.56759 ± 0.04363
AP	DECEMBER	0.95***	0.67678 ± 0.05858
	MARCH	0.96***	0.61552 ± 0.04927
	JUNE	0.96***	0.68035 ± 0.05648
	SEPTEMBER	0.97***	0.63402 ± 0.04451
HT	DECEMBER	0.76***	0.37440 ± 0.07411
	MARCH	0.85***	0.29193 ± 0.05190
	JUNE	0.95***	0.34827 ± 0.03103
	SEPTEMBER	0.84***	0.30097 ± 0.05377

*** Significant at 0.1 % level.

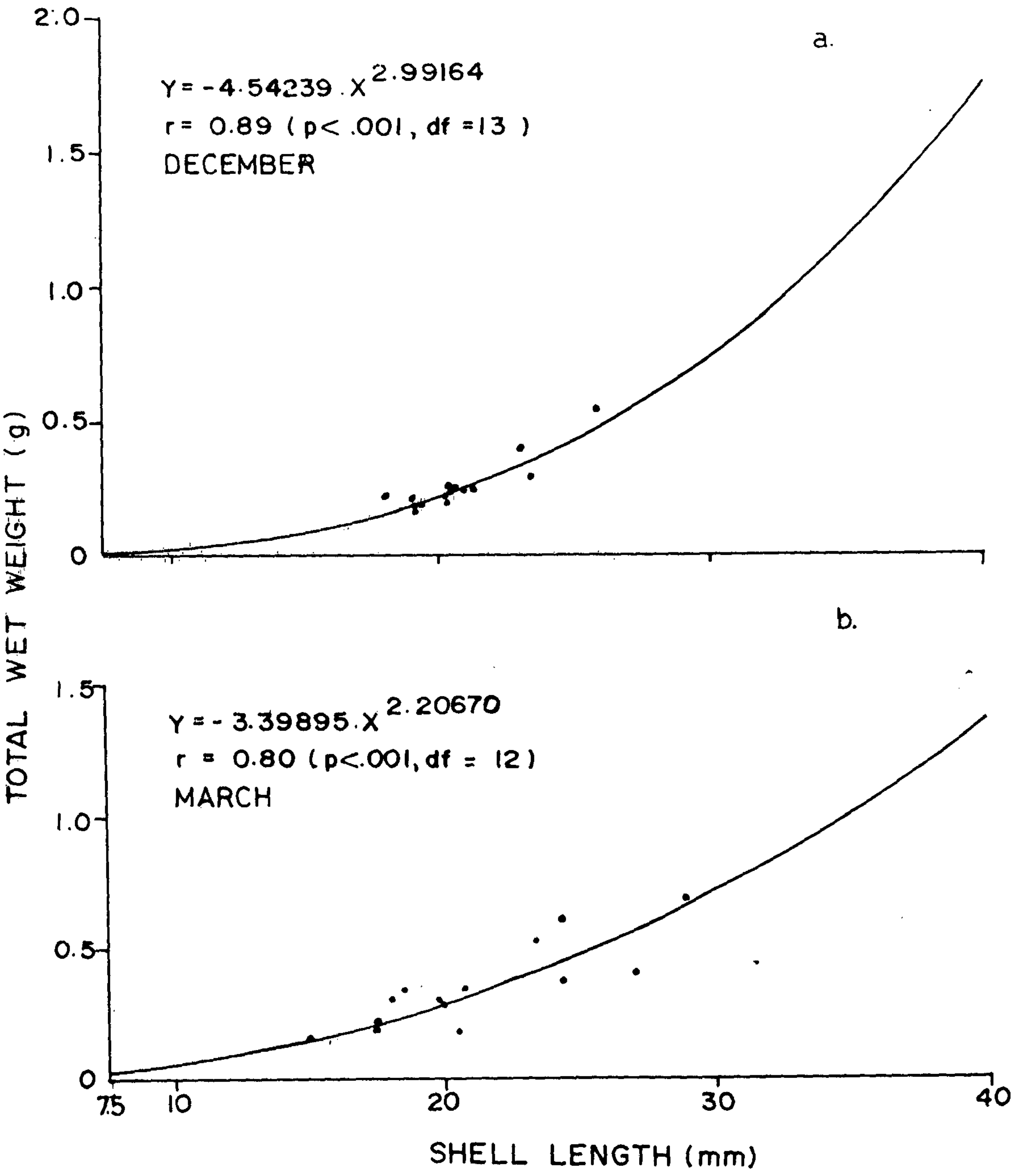


Fig. 15. The relationship between shell length and total wet weight for December (a) and March (b).

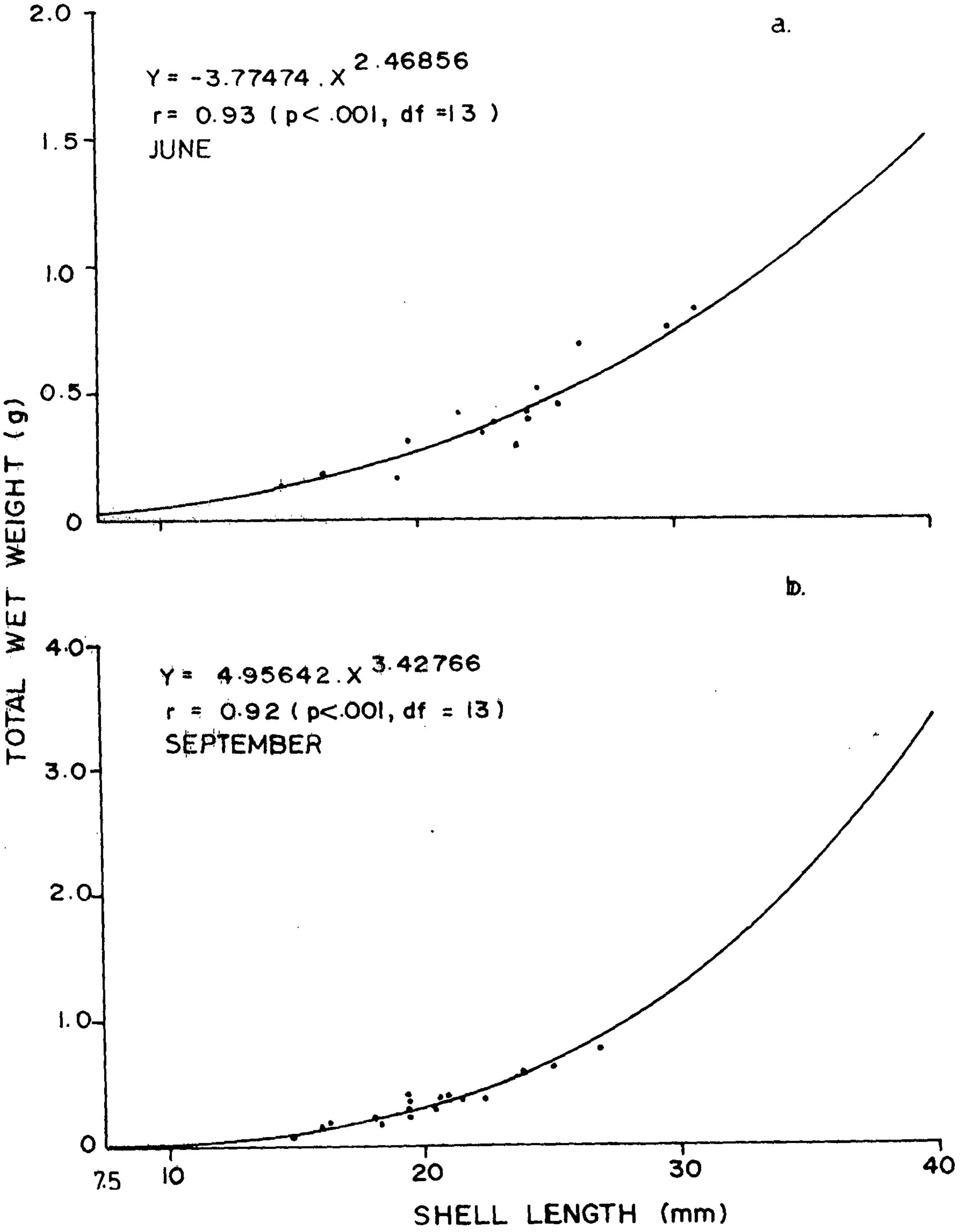


Fig. 16. The relationship between shell length and total wet weight for June (a) and September (b).

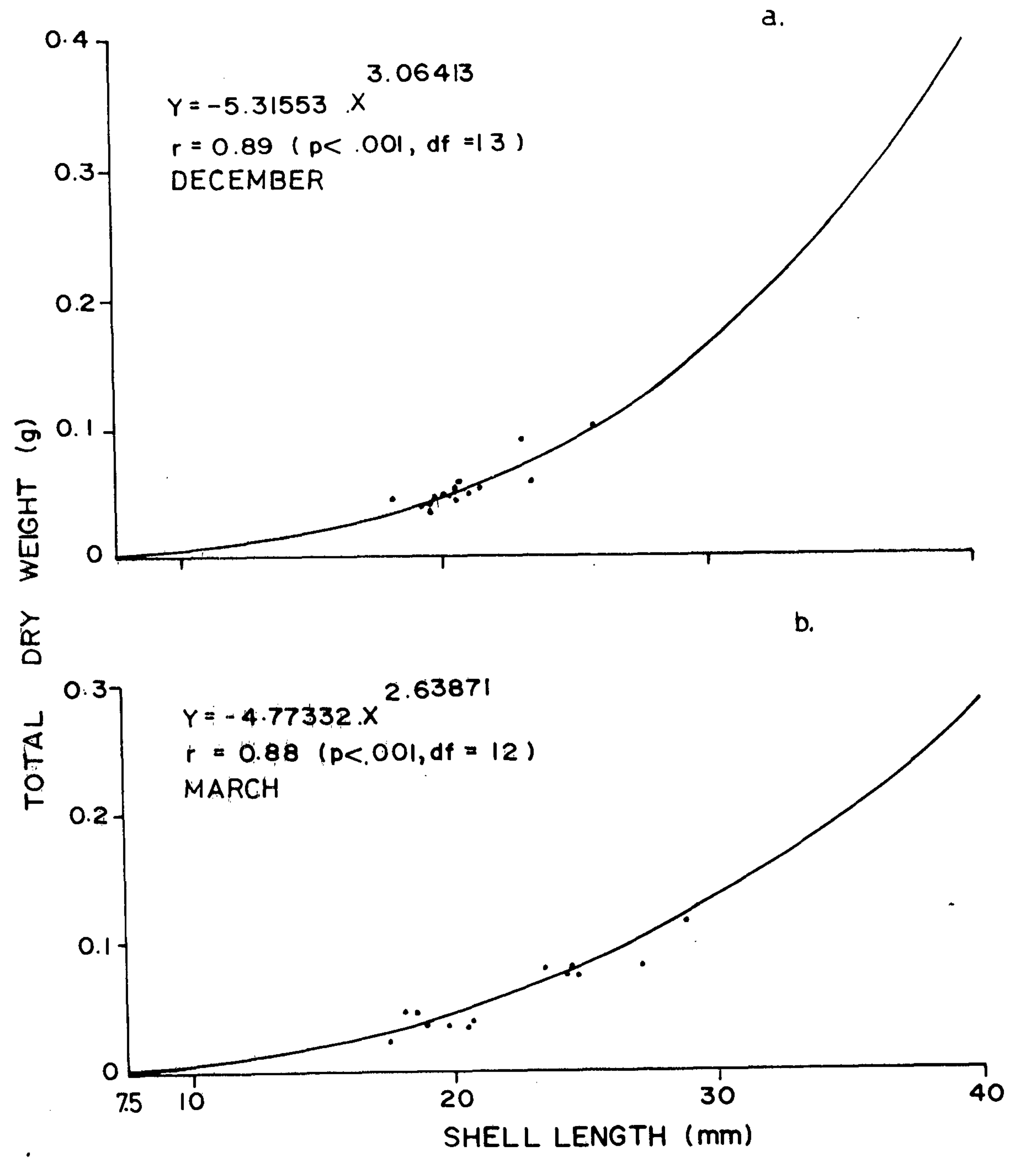


Fig. 17. The relationship between shell length and total dry weight for December (a) and March (b).

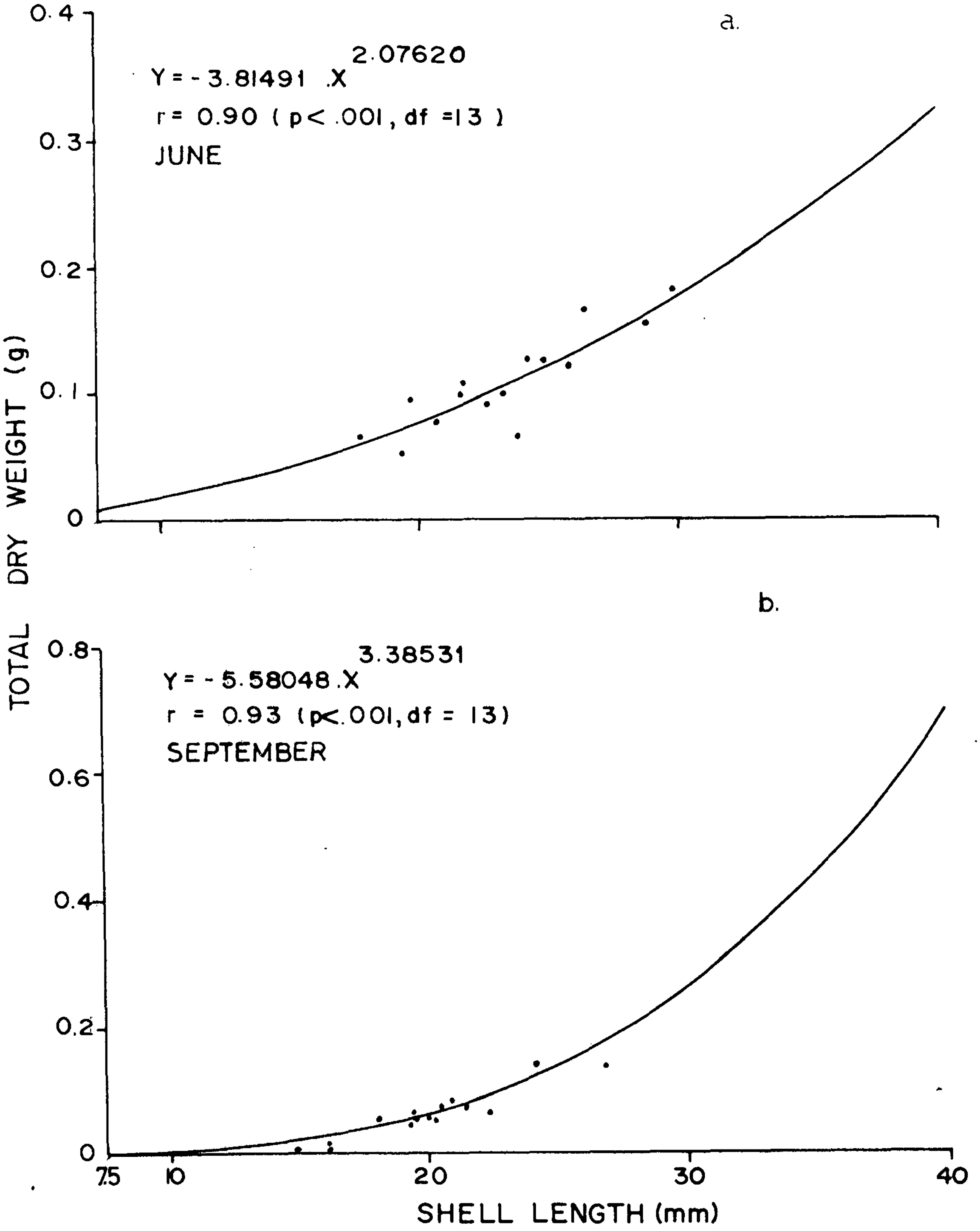


Fig. 18. The relationship between shell length and total dry weight for June (a) and September (b).

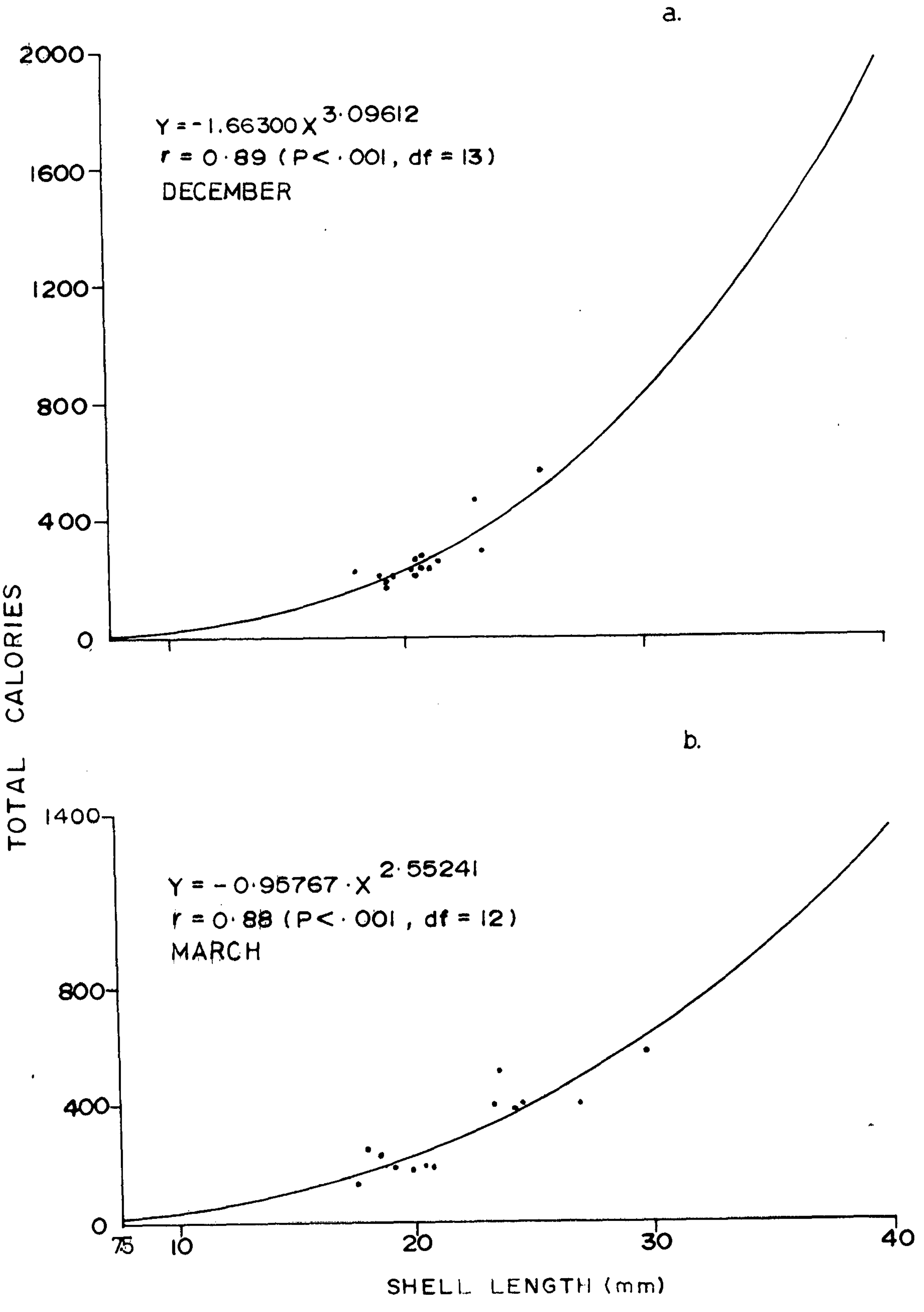


Fig. 19. The relationship between shell length and total calories for December (a) and March (b).

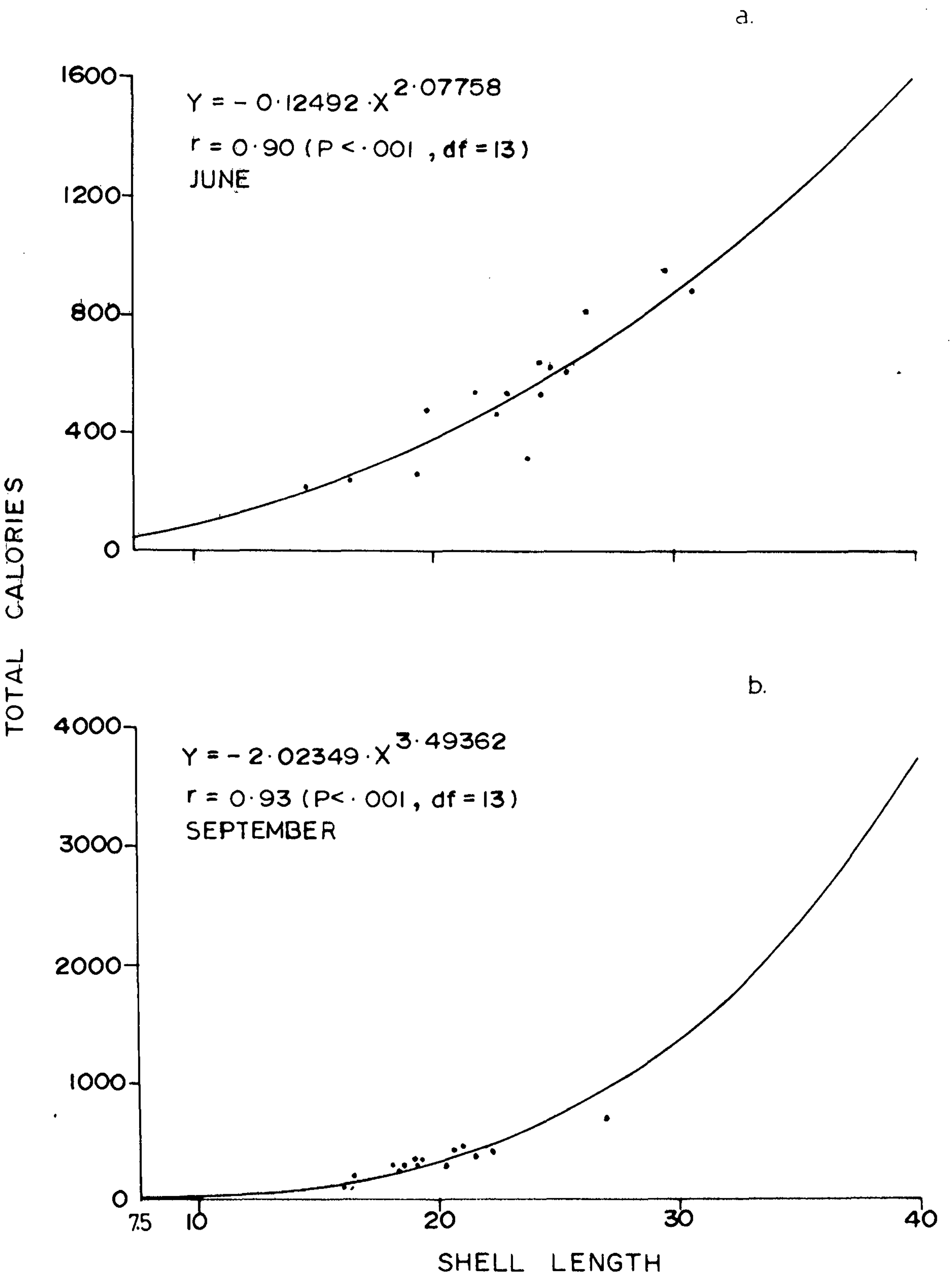


Fig. 20. The relationship between shell length and total calories for June (a) and September (b).

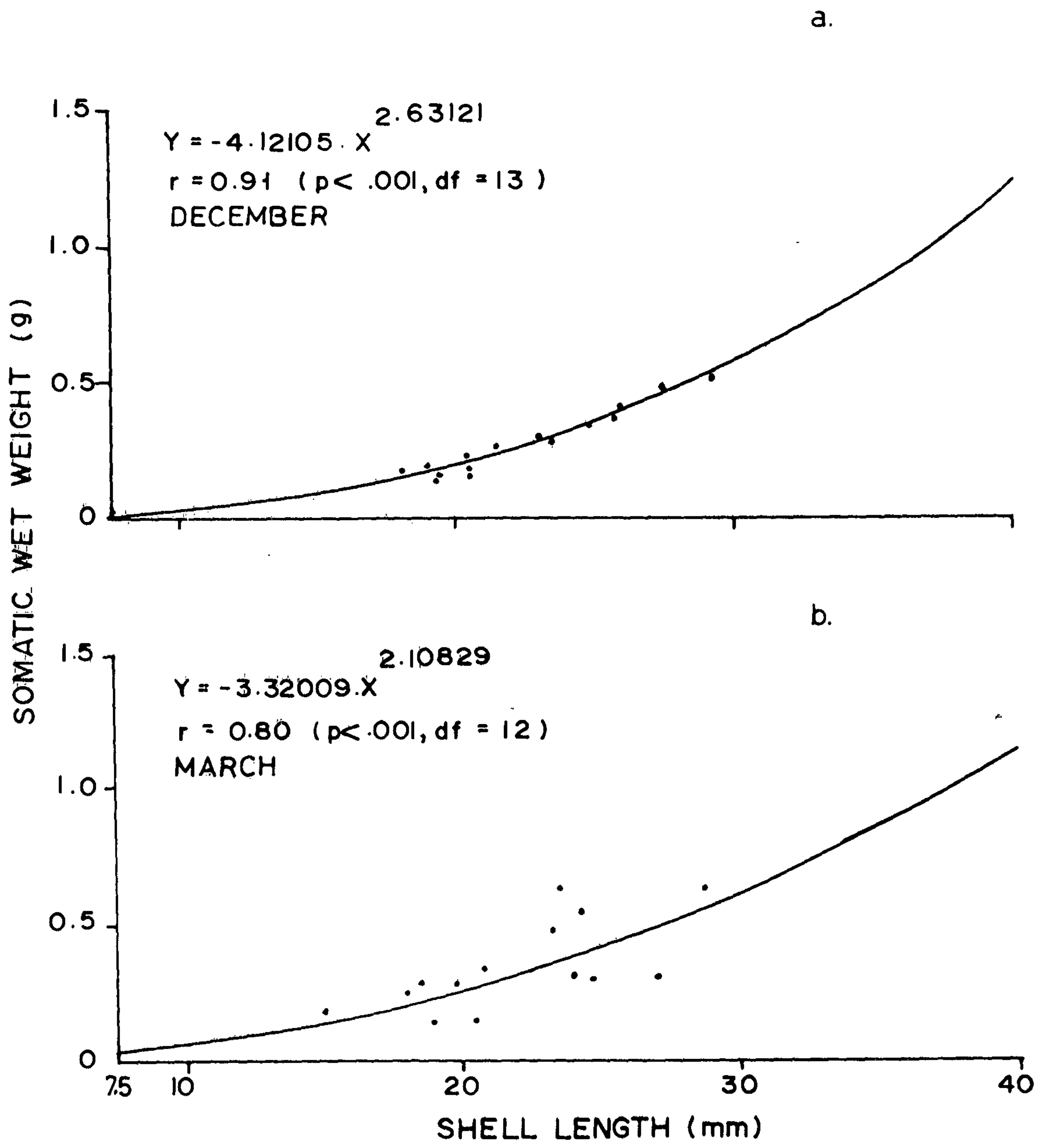


Fig. 21. The relationship between shell length and somatic wet weight for December (a) and March (b).

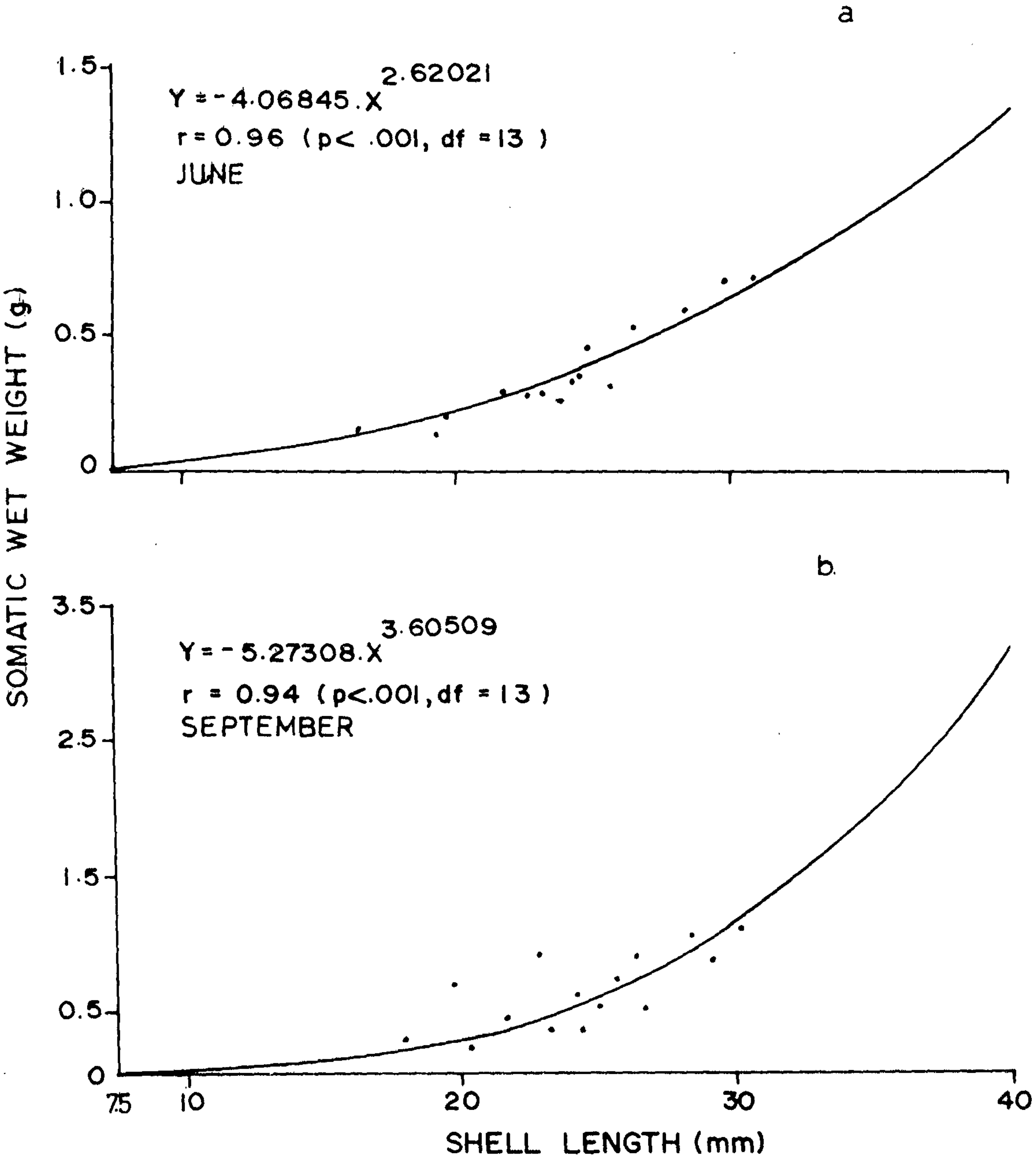


Fig. 22. The relationship between shell length and somatic wet weight for June (a) and September (b).

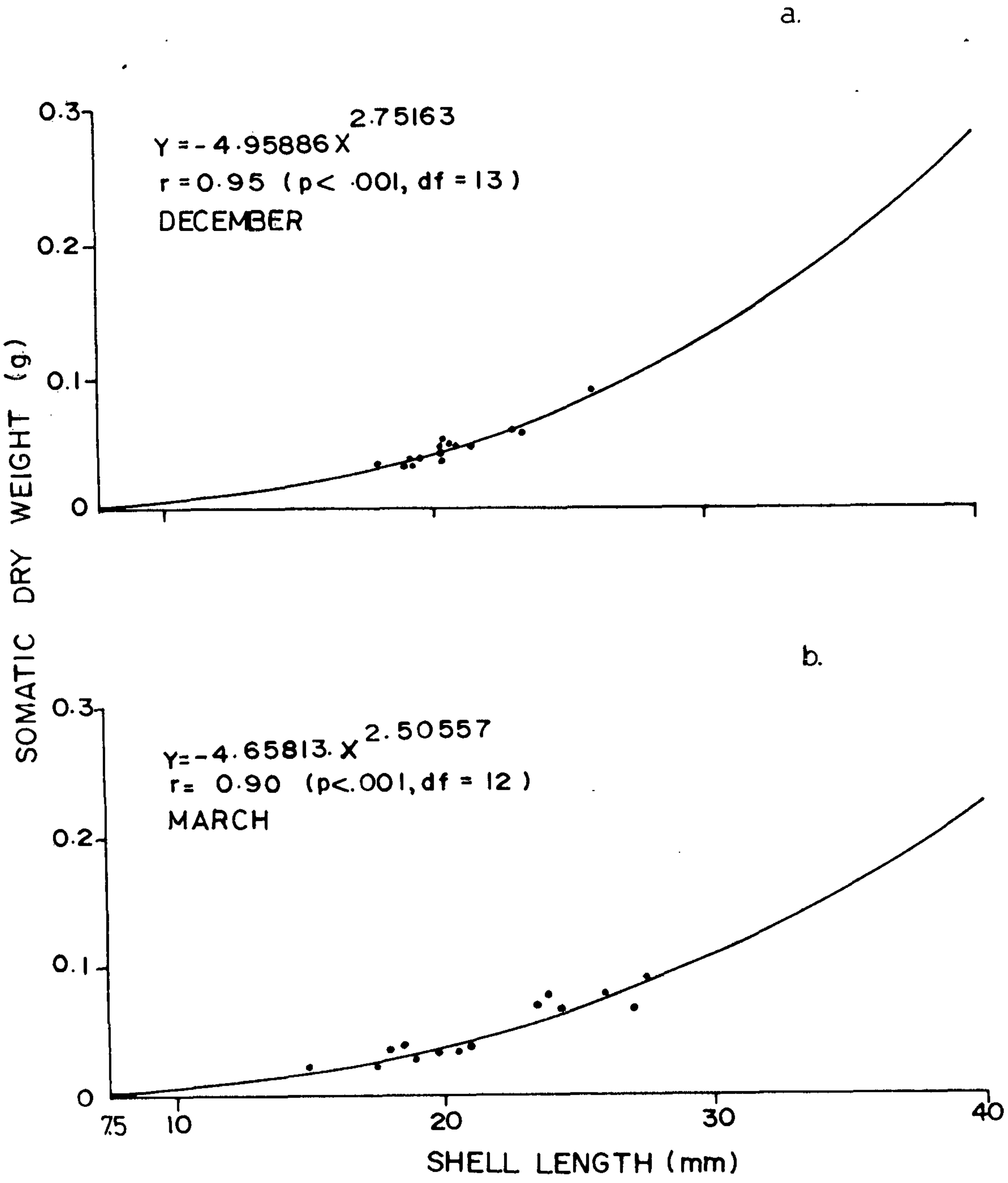


Fig. 23. The relationship between shell length and somatic dry weight for December (a) and March (b).

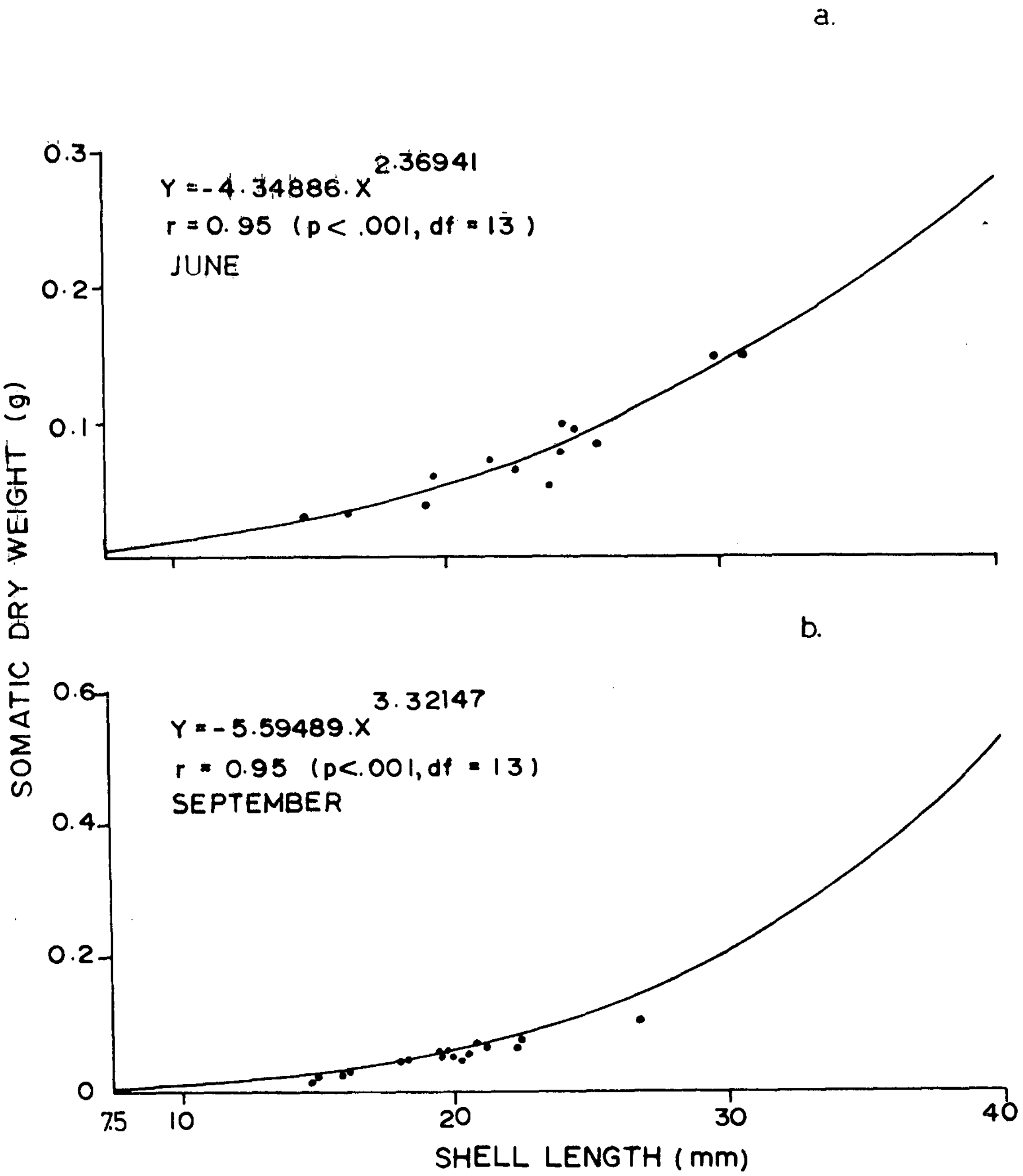


Fig. 24. The relationship between shell length and somatic dry weight for June (a) and September (b).

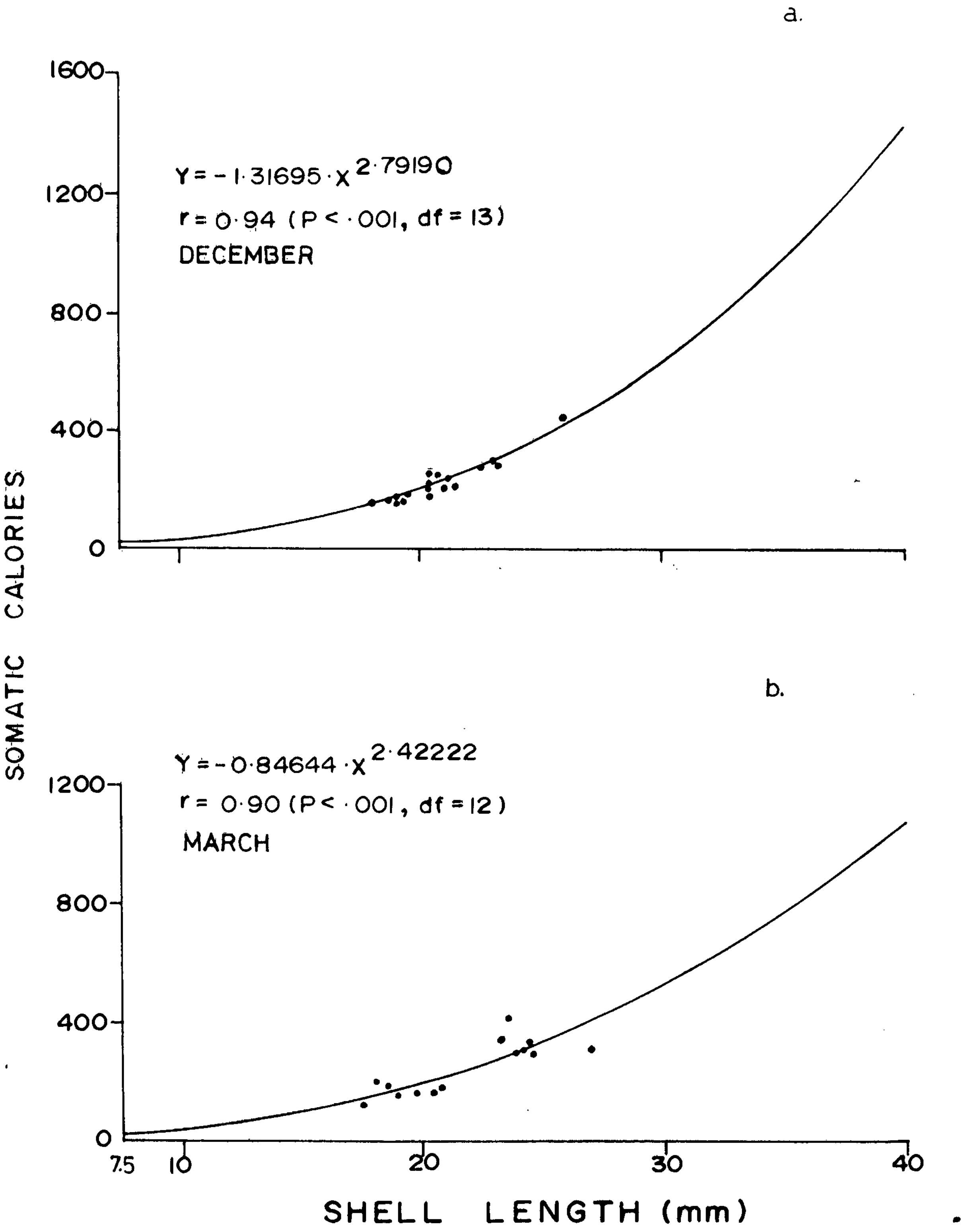


Fig. 25. The relationship between shell length and somatic calories for December (a) and March (b).

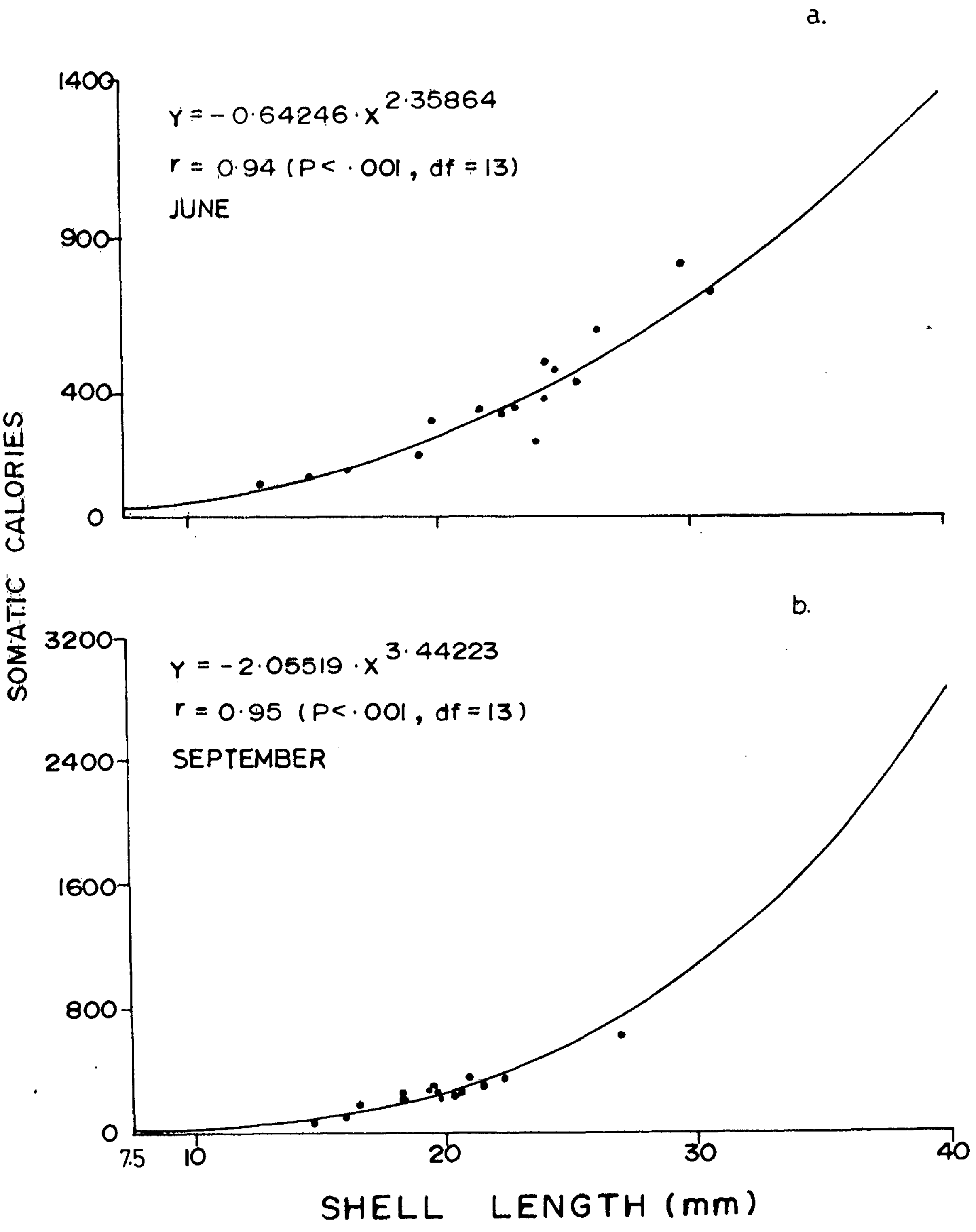


Fig. 26. The relationship between shell length and somatic calories for June (a) and September (b).

TABLE 4

Results of the non-linear regression analysis (± S.E.) carried out between shell length and various tissue parameters.

PARMETER	MONTH	r	b ± S.E
TOT WWT	DECEMBER	0.89***	2.99164 ± 0.43212
	MARCH	0.80***	2.20670 ± 0.59887
	JUNE	0.93***	2.46856 ± 0.27923
	SEPTEMBER	0.92***	3.42766 ± 0.40011
TOT DWT	DECEMBER	0.89***	3.06413 ± 0.44291
	MARCH	0.88***	2.63871 ± 0.40220
	JUNE	0.90***	2.07620 ± 0.26340
	SEPTEMBER	0.93***	3.38531 ± 0.36093
TOT CAL	DECEMBER	0.89***	3.09612 ± 0.45973
	MARCH	0.88***	2.55241 ± 0.39412
	JUNE	0.90***	2.07758 ± 0.28547
	SEPTEMBER	0.93***	3.49362 ± 0.37966
SOM WWT	DECEMBER	0.91***	2.63121 ± 0.32645
	MARCH	0.80***	2.10829 ± 0.62218
	JUNE	0.96***	2.62021 ± 0.22097
	SEPTEMBER	0.94***	3.60509 ± 0.34702
SOM DWT	DECEMBER	0.95***	2.75163 ± 0.26303
	MARCH	0.90***	2.50557 ± 0.34578
	JUNE	0.95***	2.36941 ± 0.20860
	SEPTEMBER	0.95***	3.32147 ± 0.29516
SOM CAL	DECEMBER	0.94***	2.79190 ± 0.27591
	MARCH	0.90***	2.42227 ± 0.33477
	JUNE	0.94***	2.35864 ± 0.24212
	SEPTEMBER	0.95***	3.44223 ± 0.30682

*** Significant at 0.1% level.

there are variations in the estimates for the four months sampled. . The difference between total and somatic weight/calories gave an estimate of gonadal biomass. These results are useful for the nondestructive estimation of biomass from shell size data. These were used to estimate the biomass of the natural population of *C. radiata* at Anjuna which in turn was used to estimate production rates of the natural population.

3.5 SEXUAL DIFFERENCES

Sexes in limpets are separate. They do not exhibit any externally visible secondary sexual characters. The gonadal weight of limpets with a shell length of around 10mm is negligible. and steeply rises as it attains a shell size of around 15mm. This suggests that sexual maturity is attained when the limpet attains a shell length between 10-15mm.

The variation of the gonadal index, calculated in terms of wet weight. dry weight and calories and the 95% confidence limits is shown in Fig. 27. It can be seen that the index was high during June and September and low in March and December, suggesting that spawning activity is low in June and September.

The sex ratio observed during the different months and for the whole year is shown in Fig 28. The ratio was 4:11; 6:8; 11:4 and 7:8 for males and females for December, March, June and September respectively. Unequal ratios was due to the small

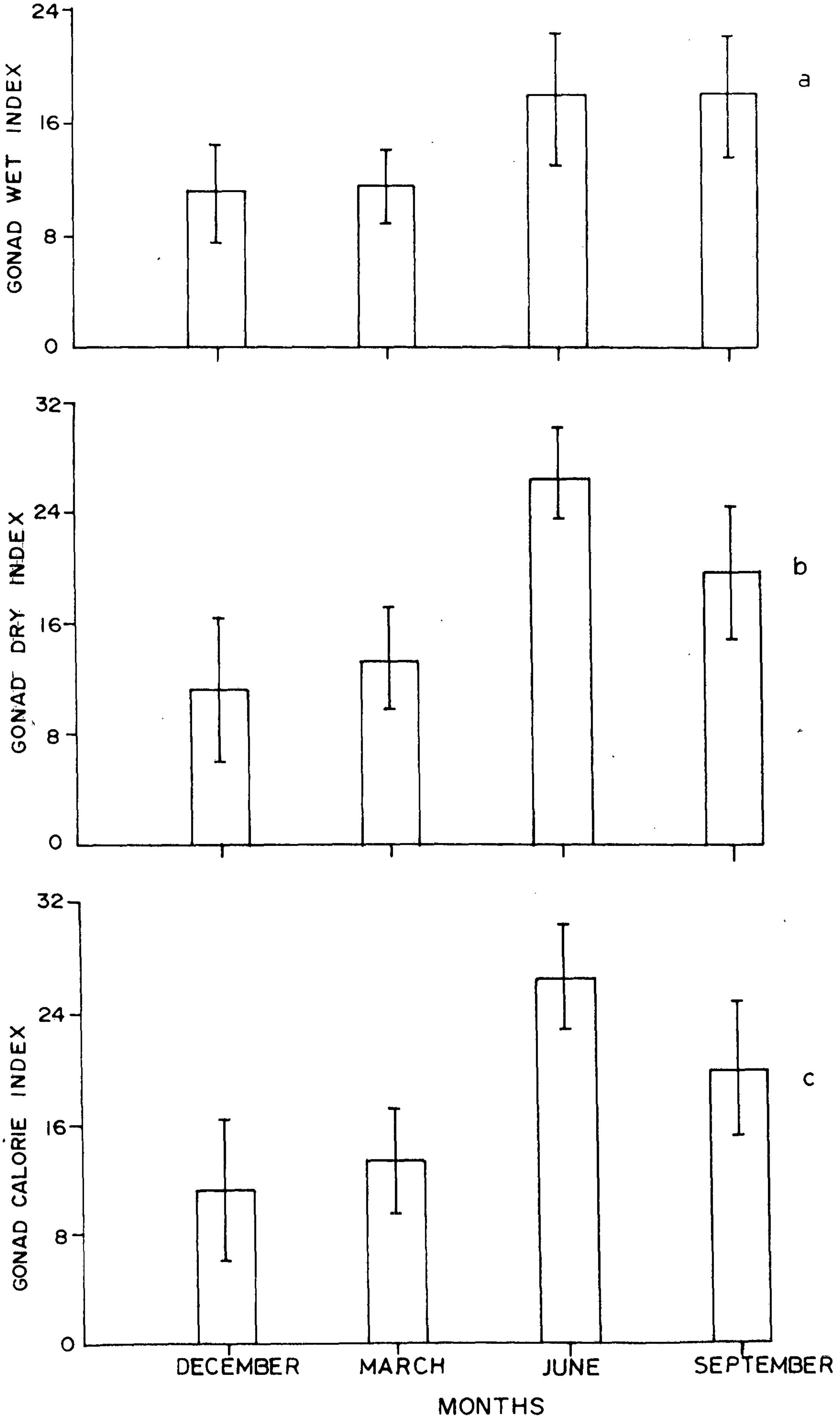


Fig. 27. Seasonal variation in gonadal index (± S.E.) in wet weight (a) dry weight (b) calorie (c).

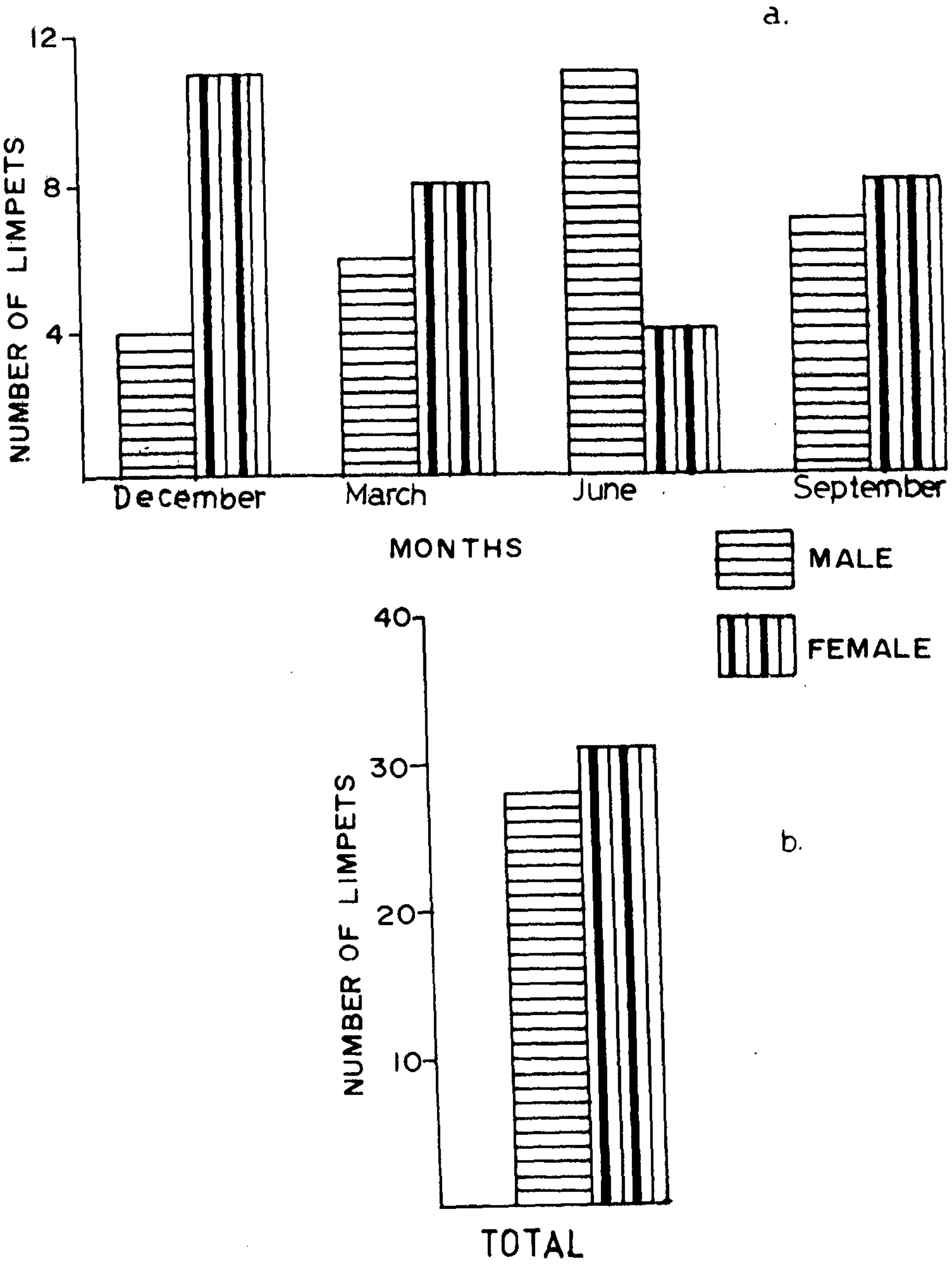


Fig. 28. Sex ratio recorded for different months (a) and for the total period (b).

sample size. As noted elsewhere, sex could be determined only after examining the gonad. When the all data is pooled, the ratio is 28:31 implying a 1:1 relationship.

The shell characteristics of male and female limpets are tabulated in Table 5. Results of the Student's *t* test revealed that there were no statistically significant differences between sexes. The mean calorific values of somatic and gonadal tissue in male limpets were 4978 cal/g and 5052 cal/g respectively while that of female limpets were 5015 cal/g and 5100 cal/g respectively. These values are comparable with that of other limpets. Fatima and Temuri (1992) obtained a value of 4.91 kcal for soft tissues of *C. radiata*. Parry (1982b) reported values ranging from 4600 to 6400 cal/g in four species of limpets.

3.6 LABORATORY OBSERVATIONS

Limpets could be maintained in the laboratory for short periods. The longest duration they survived was four months. Smaller limpets adapted much better to laboratory conditions compared to larger ones.

3.6.1 FEEDING

The digestive system and the radular teeth of *C.radiata*, as dissected, are shown in Fig. 29. The gut of *C. radiata* can be

TABLE 5

Results of the t test carried out between male and female limpets.

	MALES (N = 28)				FEMALES (N = 31)				
Parameter	Min.	Max.	Mean	S. D.	Min.	Max.	Mean	S. D.	t value*
Length (mm)	14.95	30.85	21.82	3.38	14.80	29.80	21.85	3.44	0.0337
Width(mm)	12.35	26.20	18.09	2.99	14.80	24.80	17.59	3.20	0.6173
AA (mm)	7.95	17.10	11.63	1.85	7.75	20.10	11.64	2.49	0.0174
AP (mm)	10.45	20.80	15.84	2.25	10.90	21.60	15.49	2.40	0.5585
HT (mm)	4.35	9.60	6.75	1.07	4.30	10.45	6.69	1.30	0.2240
Tot.wet wt.(g)	0.149	0.840	0.380	0.173	0.077	0.778	0.331	0.175	1.0644
Tot.dry wt.(g)	0.024	0.185	0.082	0.037	0.016	0.184	0.071	0.040	1.1127
Tot. cal.	134	916	410	186	74	969	354	204	1.0000
Tot.cal/g	4952	5469	5210	5053	4623	5264	4944	4854	0.2069
Som. wet. wt	0.111	0.720	0.307	0.138	0.069	0.719	0.290	0.157	0.4500
Som. dry wt.	0.024	0.151	0.063	0.027	0.015	0.155	0.058	0.031	0.6705
Som.cal.	131	725	314	131	71	822	291	160	0.6263
Som cal./g	4806	5432	4978	4853	4736	5305	50	4925	0.0298

* All t values are not significant.

divided into three regions: the fore gut, mid gut and the hind gut. It is similar to that observed by Rao, (1975b) *C. radiata* has only four loops in the gut round the visceral mass in contrast to the six loops in *Patella* species (Graham, 1932; Fretter & Graham, 1962). The radular teeth consists of a central tooth flanked on the sides by two laterals (Fig. 29).

Analysis of the gut content of limpets collected from the study area revealed the presence of a variety of algal bits in various stages of digestion. The percentage composition of the various algae in the diet is presented in the Table 6. Diatoms were the main food source, forming about 40% of the diet (Table 6). *Enteromorpha* spp. was next in importance, forming 41% of the diet in April and 22% in September. Though *Chaetomorpha* sp. was not recorded in the diet in March, they formed a sizable proportion (19%) of the diet in September. Other algal genera recorded in the gut were *Centroceras* sp., *Polysiphonia* sp. *Hildenbrandia* sp., *Grateloupia* sp. and some unidentified species of blue green algae.

Subsequent observations in the laboratory also revealed that the limpets mainly fed on green algae like *Enteromorpha* spp., *Chaetomorpha* sp., besides diatoms. Limpets were seen feeding only when covered by water. When submerged, the constant and continuous motion of the mouth and radula could be observed through the walls of glass tanks.

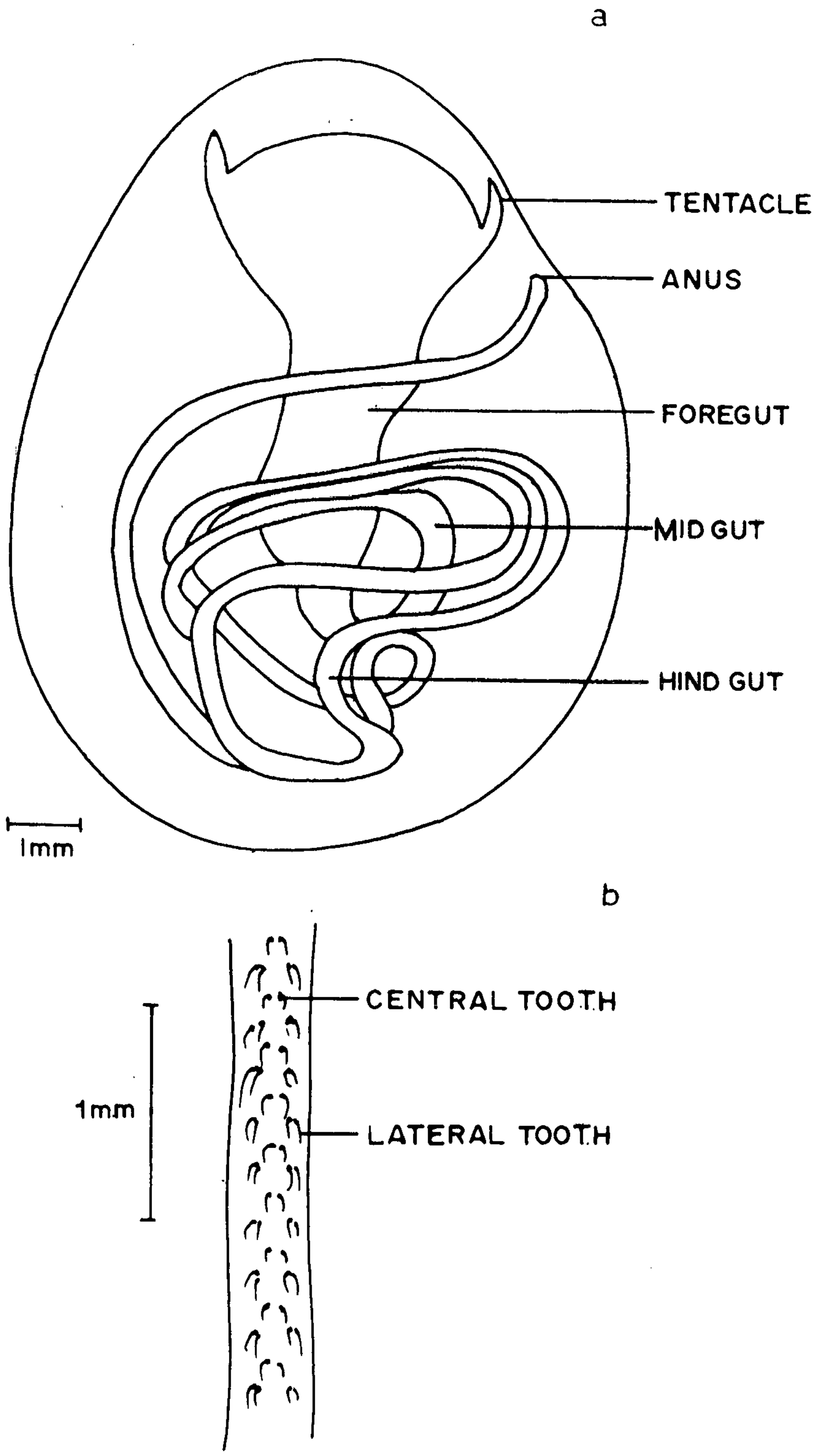


Fig. 29. The digestive system (a) and radular teeth (b) of *C. radiata*.

TABLE 6

Percentage of occurrence of different food source in the gut of *C. radiata*.

Species	March(n=5)	October(n=5)
Enteromorpha	41	22
Blue green algae	6	-
Diatoms	44	47
Centroceras	2	2
Grateloupia	1	2
Polysiphonia	-	1
Chaetomorpha	-	19
Hildenbrandia	-	4

3.6.2 SPAWNING

Spawning was observed in the laboratory in the month of December. Limpets being oviparous, development takes place outside the parent. No pairing of sexes was observed. Males were observed to spawn first, followed by females. Eggs and sperms were released from the anterior end. Sperms were released in a trail which soon dispersed. Release of eggs was a slow process, stretching to several hours. Eggs were deposited in a mass and appeared like a brown patch, dispersing as they were stirred. The fertilized eggs metamorphosed through different stages. Larval stages of *C. radiata* have been described by Rao (1975a). The last stage observed was the late veliger stage. Most of the larvae died after the last stage. Two limpets grew to a size of 2.9mm and 3.0mm in 25 days. Another limpet survived for 40 days attaining a shell length of 4.6mm.

3.7 FIELD OBSERVATIONS: MOVEMENT PATTERNS

The movement pattern of 80 limpets, as recorded in the field in February, are shown in Fig. 30 to Fig. 31. Observations were carried out for 24 hrs. Activity began when the limpets were covered by the tide. All limpets were observed to move away from the base to a different location. The daily displacement distance ranged from 19.3cm to 35.6cm, with a mean of 25.3 ± 8.15 cm (Fig. 35). Field observations, over a longer period, were once again carried out in May.

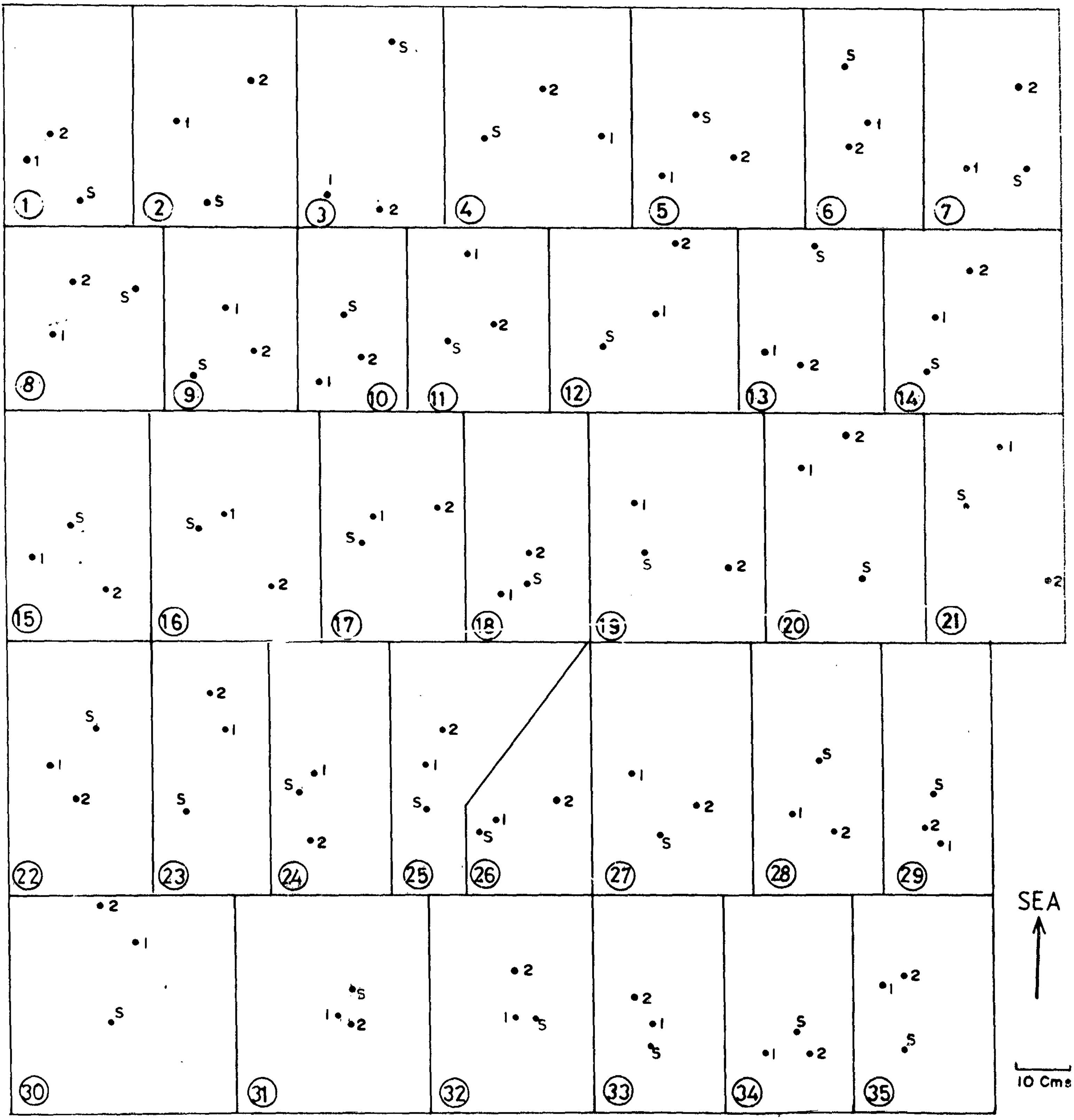


Fig. 30. The movement patterns of various limpets recorded in February (S = starting point).

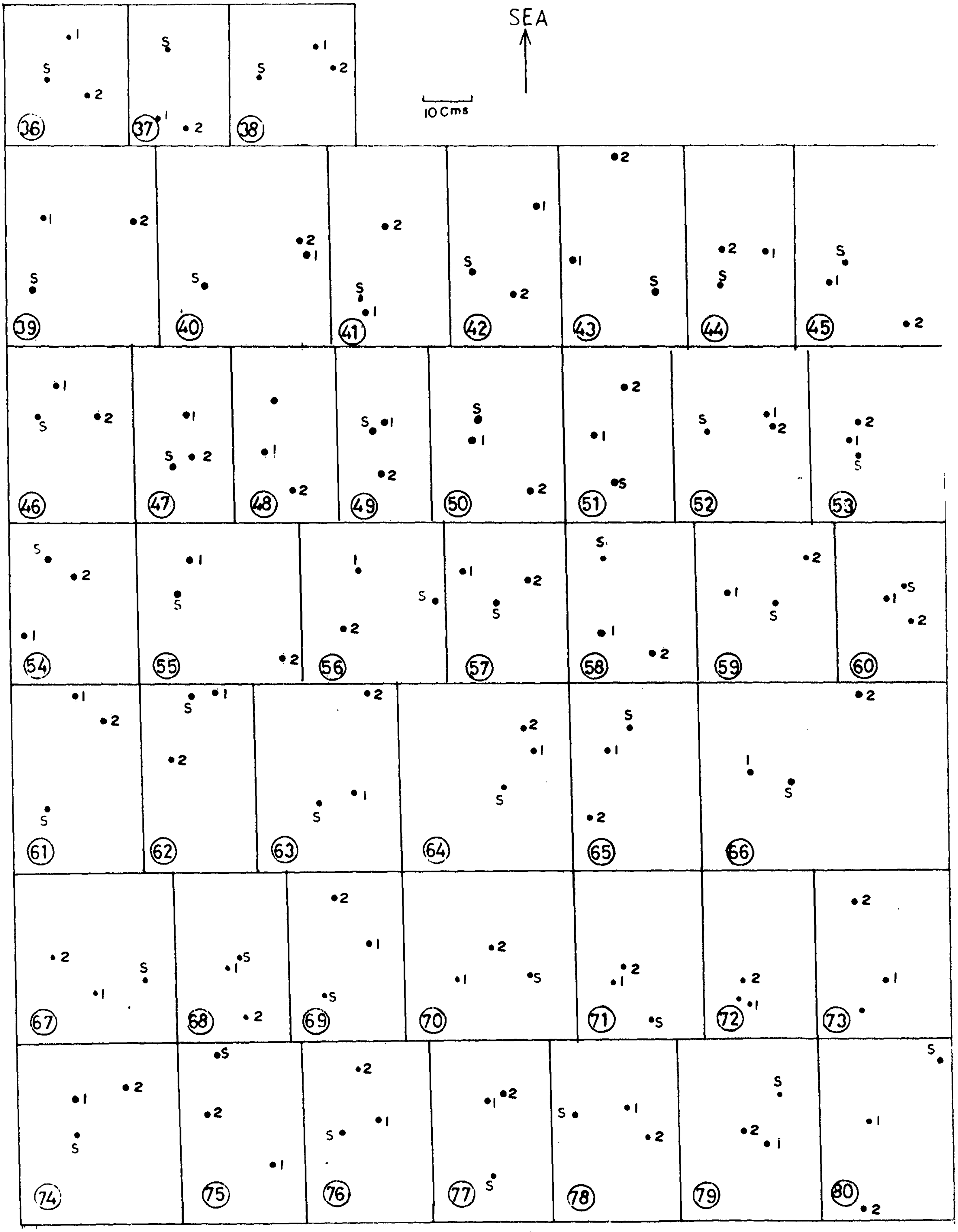


Fig. 31. The movement patterns of various limpets recorded in February (S = starting point)

The movement patterns of the 24 different limpets observed in the field on four consecutive days in May are retraced in Fig. 32 to Fig. 34. Limpets were observed to move only when covered by the tides. One obvious recognizable pattern is that most of the animals moved seaward, probably for feeding. Another observation, not recorded in the earlier field observations conducted in February, is that every marked limpet returned to its home base before the low tide approached. The home base had no scar or depression on the rock, instead it just had an outline possibly of the shell edge. Another important field observation was that the limpets oriented themselves in a slightly different angle after each excursion. It was also observed that limpets never retraced their paths on succeeding excursions.

The average displacement of individual limpets was 40.5 ± 11.10 cm/day. Displacement distances ranged from 28.2 cm/day to 50.4cm/day. The frequency distribution of distances moved from the during excursions in May are shown in Fig. 36. The frequency distribution follows a normal distribution and is slightly skewed to the left. The limpets thus appear to generally prefer shorter excursion distances.

A rosette of the frequency distribution of the angle of orientation during succeeding excursions are depicted in Fig. 37. Results indicate a preference for narrower angles (between 0-180°).

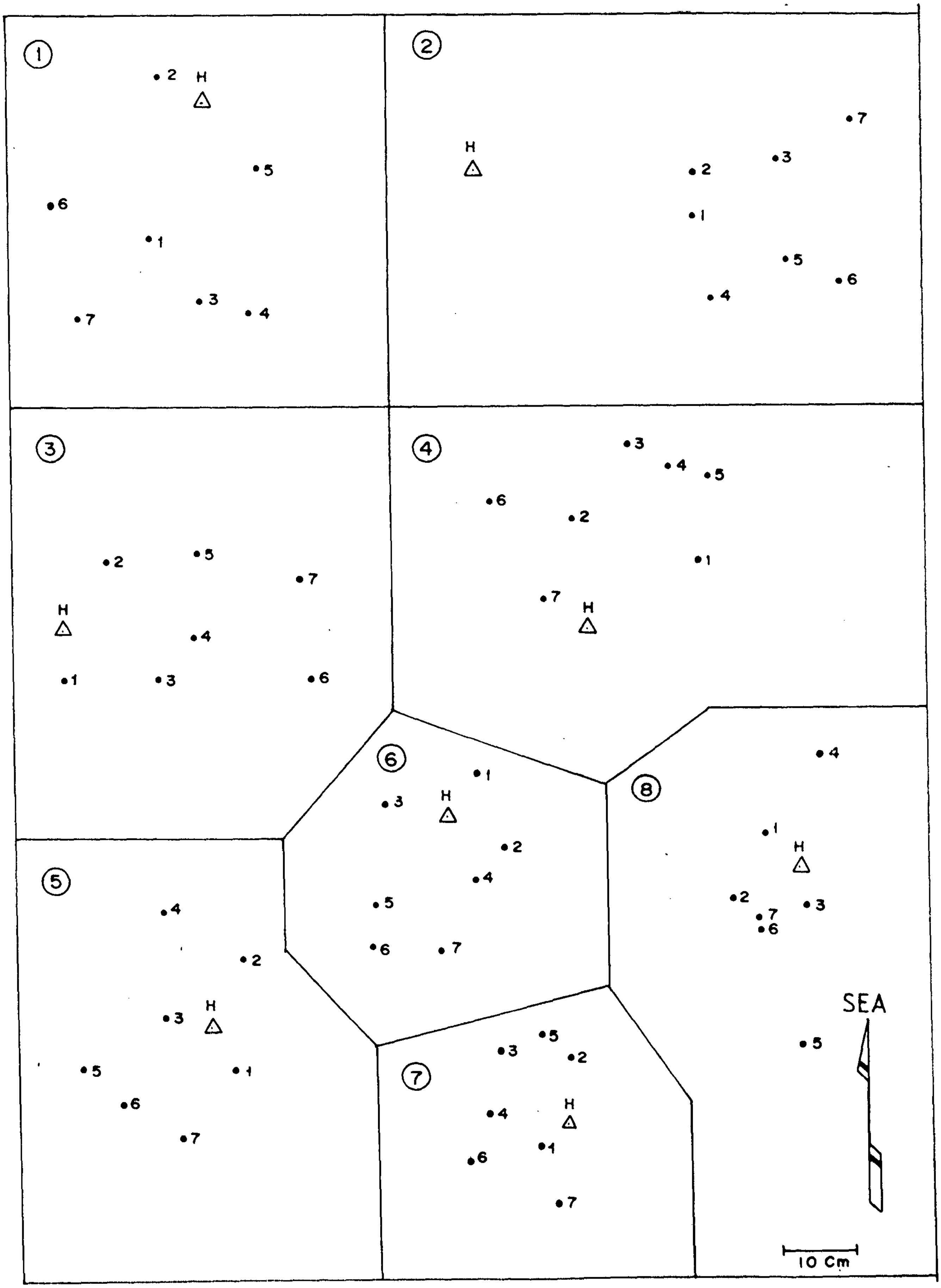


Fig. 32. The movement patterns of various limpets recorded in May (H = home).

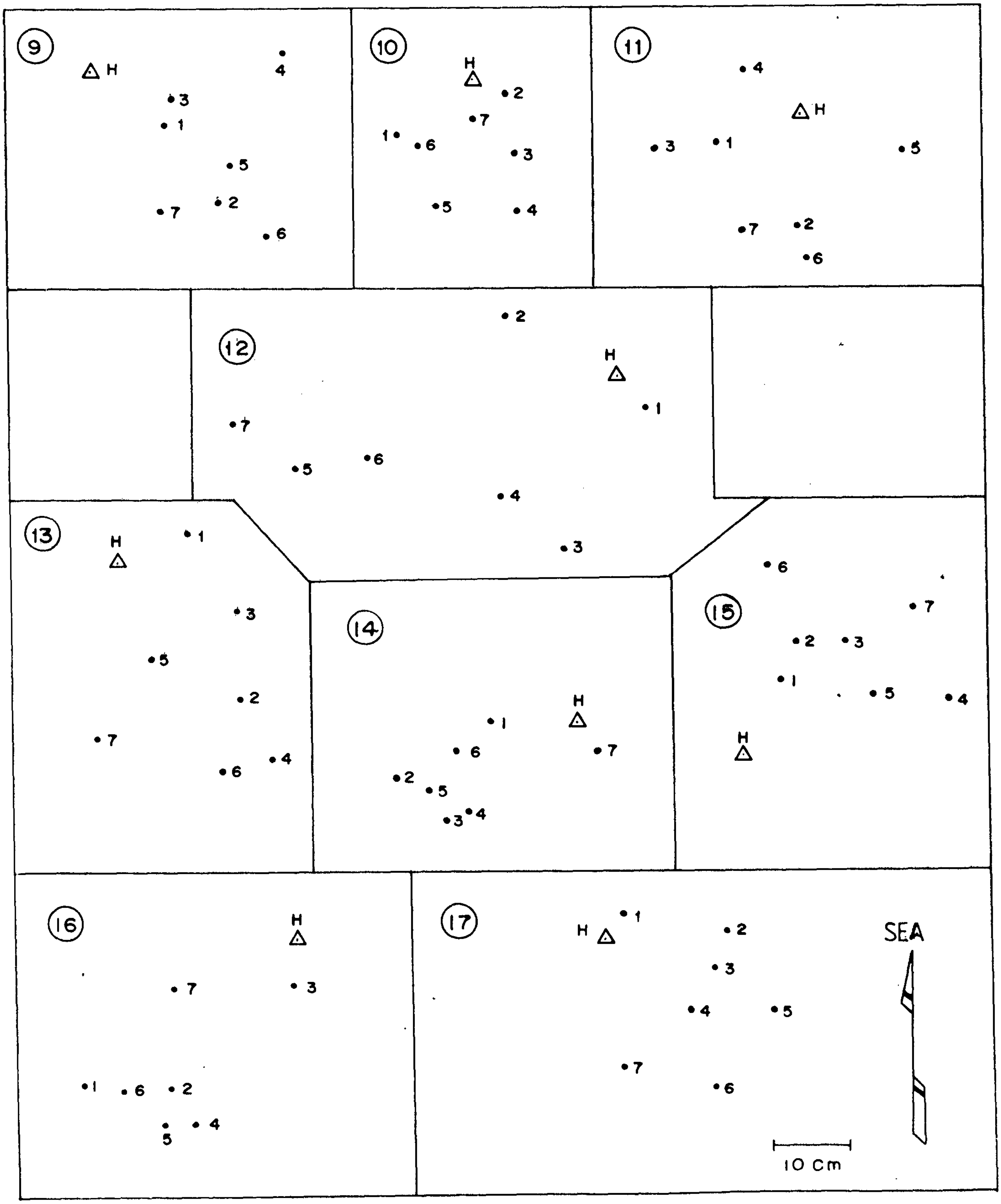


Fig. 33. The movement patterns of various limpets recorded in May (H = home).

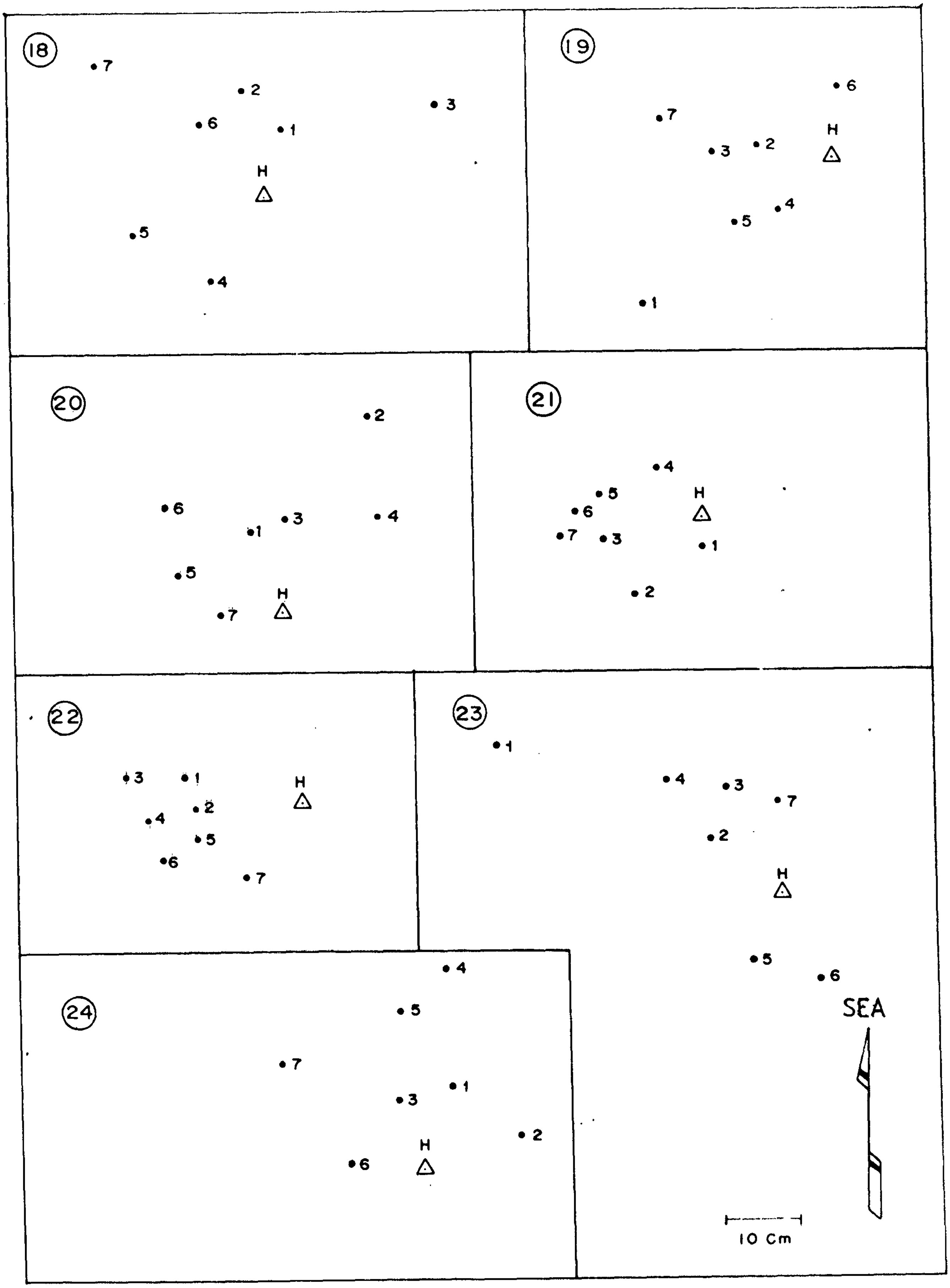


Fig. 34. The movement patterns of various limpets recorded in May (H = home).

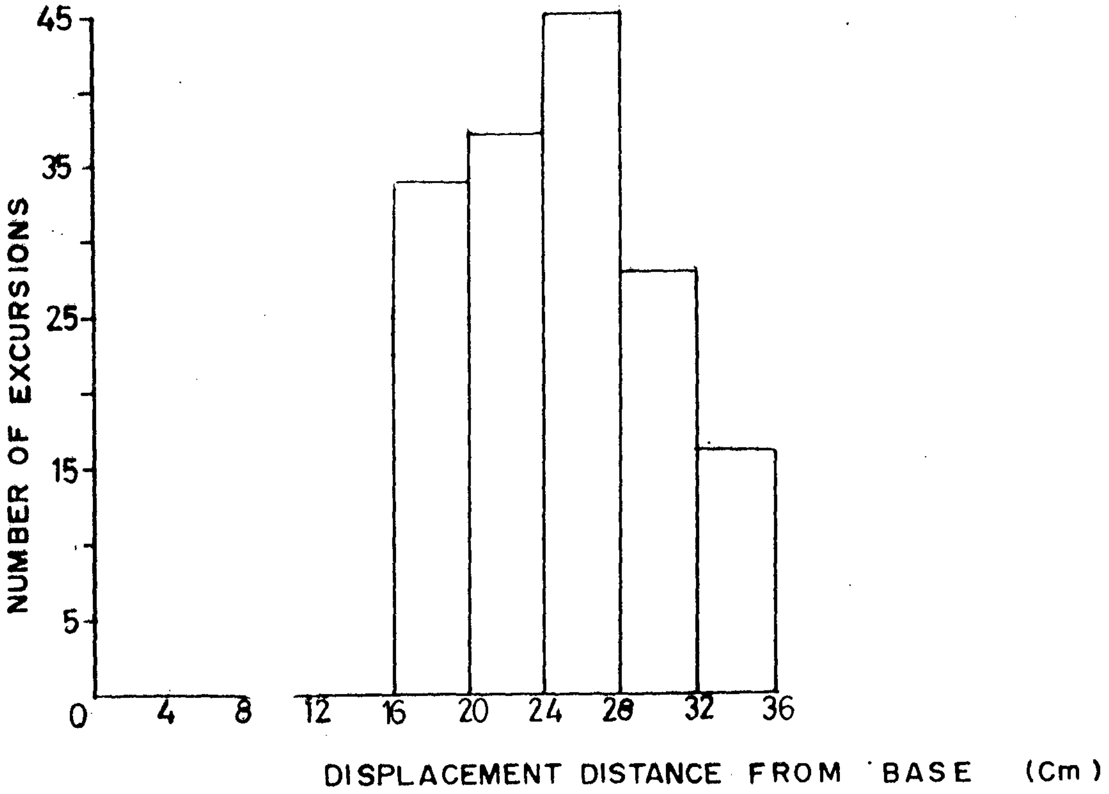


Fig. 35. The frequency distributions of displacement distances from the starting point of *C. radiata* recorded in February.

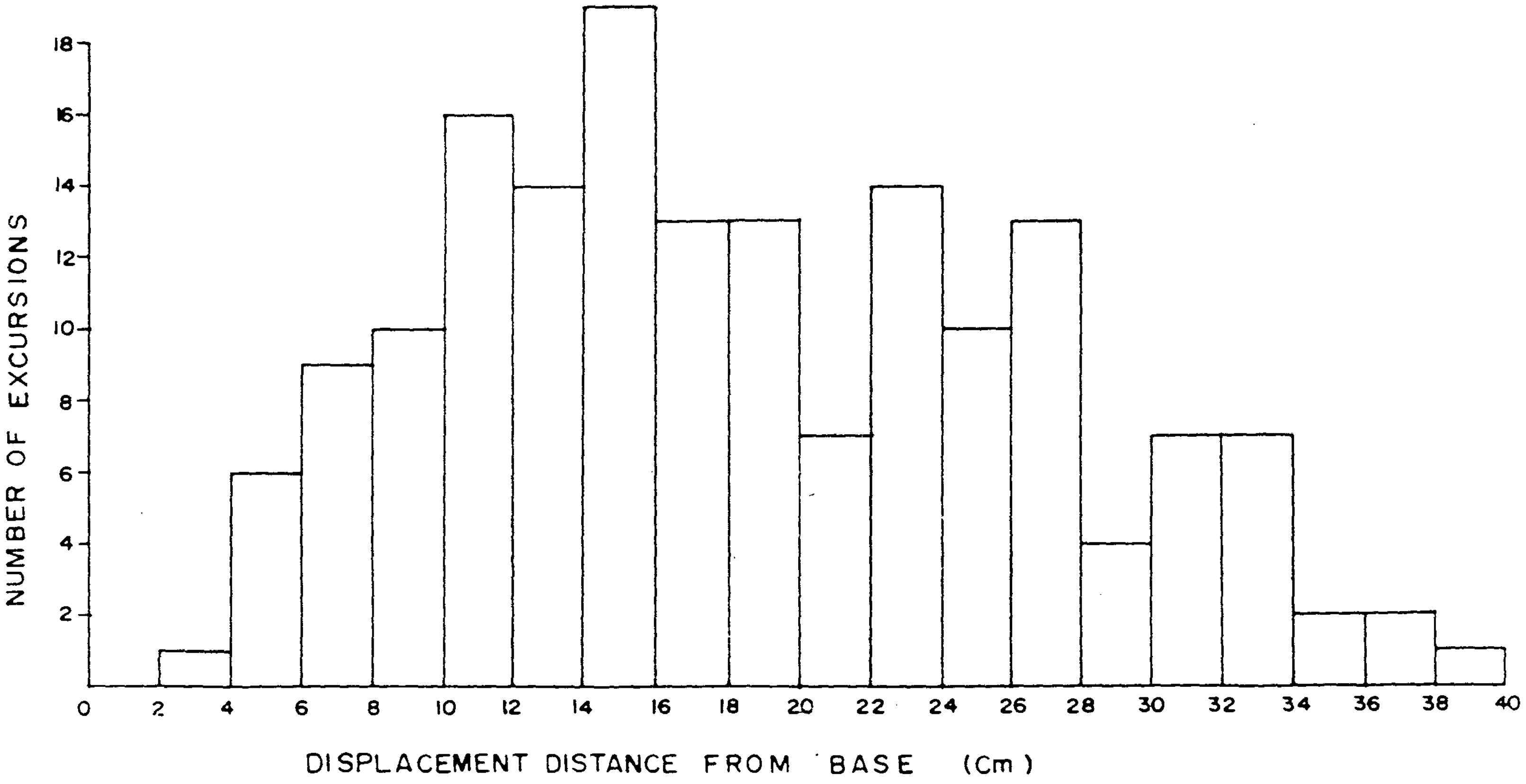


Fig. 36 The frequency distributions of displacement distances from the home base of *C. radiata* recorded in May.

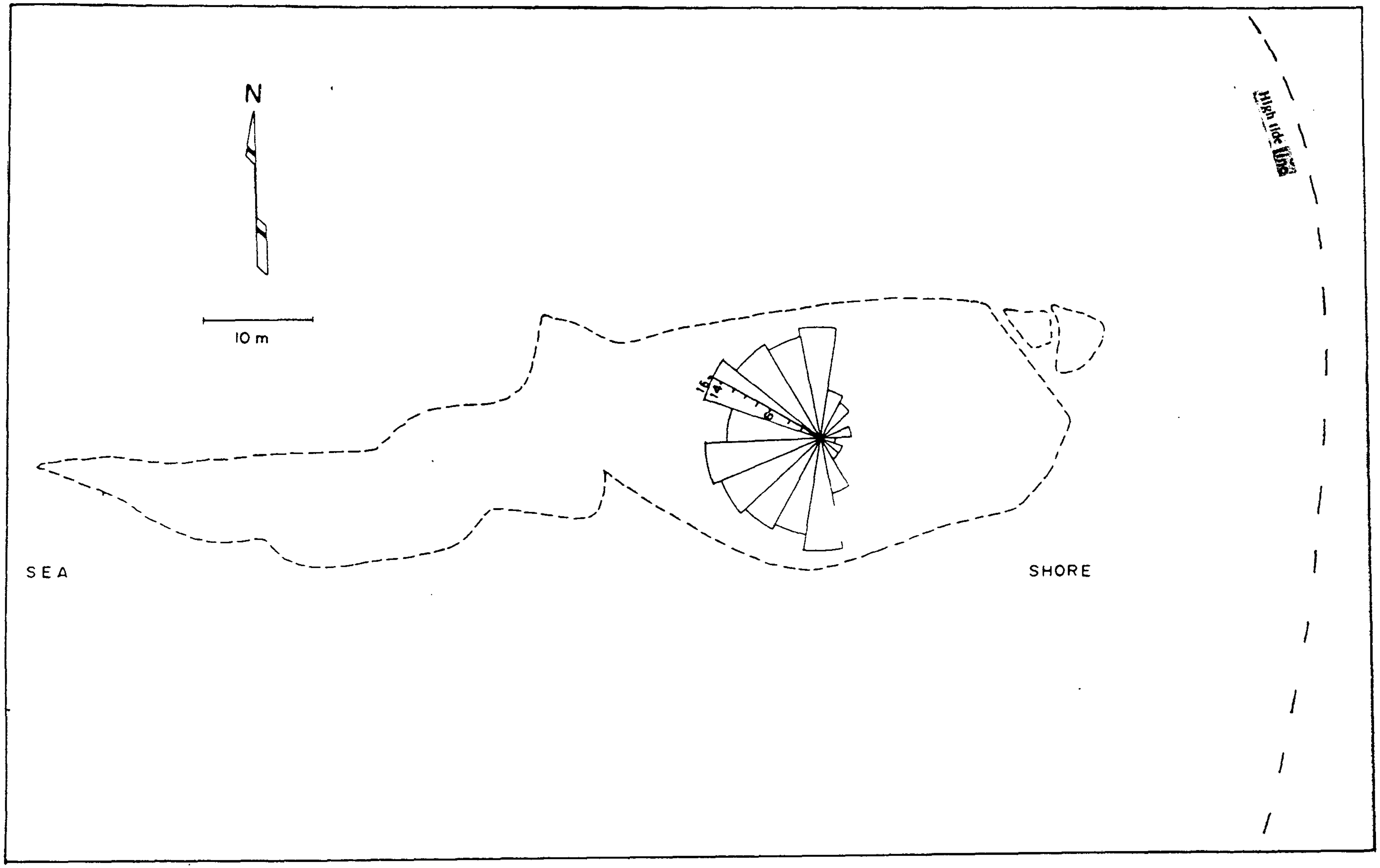


Fig. 37. Frequency of the angle of orientation recorded during succeeding excursions in May.

3.8 DISCUSSION:

3.8.1 DISTRIBUTION OF THE LIMPETS

Cellana radiata is one of the most common limpet species occuring in tropical regions. In India they have been recorded along the Waltair coast (Rao & Ganapati, 1967), Madras harbour (Sukumaran & Krishnaswamy, 1961), South Kerala coast (Suryanarayan & Nair, 1975), Saurashtra coast (Prasad & Mansuri, 1982) and the Goa coast (Balamani, 1990; Coutinho, 1993). Their worldwide taxonomical distribution has been reviewed by Powell (1973).

The distribution of *C. radiata* at Anjuna indicated that it is mainly a midtidal inhabitant. They tended to avoid the upper and lower tidal levels, where they are very scarce. Similar observations were reported earlier (Peter, 1989; Balamani, 1990; Coutinho, 1993). Earlier studies showed that along the gradient, maximum desiccation occured at the high shore (Balamani, 1990). Physical factors thus seem to be determining the upper limits of *C. radiata* at Anjuna. Davies (1970) observed that increasing temperatures resulted in the heating up of the limpet by absorption or conduction from the surrounding environment, inflicting a great stress upon them and thus reducing their upward distribution. Besides, an increase in temperature disrupts their metabolic activities (Branch, 1981). In the present study, the high shore regions of Anjuna had a concentration of limpets in crevices and tide pools, as an adaptatation against the harsh physical stresses prevailing in this zone.

The lower tidal levels at Anjuna are increasingly occupied by sessile animal species such as *Saccostrea* sp., *Pallasia* sp., *Chthamalus* sp. (Peter, 1989) and algae such as *Sargassum* sp., *Gelidium* sp., *Hypnea* sp. and *Gracilaria* sp. (Acharya, 1989). The competition for space here is thus intense. Generally, limpets limit the encroachment of algae (Branch, 1985) though the reverse has also been reported (Simpson, 1976). At lower tidal levels where algal production remains unmatched, limpets often fall out of competition (Branch, 1985). Similar pattern was also visible at Anjuna. In the lower shore, limpets occupied whatever space that was available and all these limpets had an overgrowth of algae. Some limpets also had barnacles, *Chthamalus* sp., settled on their shells illustrating the intensity of competition for space.

The upper limit of distribution of intertidal organisms is generally governed by physical factors *viz.* temperature, desiccation, salinity, osmoregulation and wave action (Southward, 1958; Davies, 1969; Wolcott, 1973; Branch, 1975; Choat, 1977) while their lower limits are determined by biological factors such as predation, behavioural response and inter and intra specific competition (reviewed in Underwood, 1979).

A gradation in size of *C. radiata* in an upshore direction was noted in the study area (Balamani. 1990). Limpets at the upper shore were relatively larger then their counterparts on the lower shore. Similar observations were also made by Choat and Black (1979) in their studies on *Collisella digitalis*. Vermeij (1973), in support of his findings stated that a larger size was more advantageous at the high shore. Lowell (1984) elaborated that as water loss was inversely proportional to body size, larger bodies tended to lose water more slowly and hence desiccation is particularly a severe problem for smaller limpets. As a result. smaller limpets are restricted to the lower shore where water loss is minimal. Variations may also arise as a result of density dependent growth rates (Creese, 1980), recruitment at lower tidal levels (Fletcher, 1984a), wave impact (Thompson, 1980) and interspecific competition (Lewis & Bowman, 1975).

3.8.2 VARIATIONS IN SHELL CHARACTERISTICS

Differences in shell characteristics between sexes were small and not statistically significant. Sizes of males and females overlapped. Orton *et. al.* (1956), in their studies on *Patella vulgata*, reported that larger sizes were predominantly females while smaller size to be males. This led them to suggest that *P. vulgata* was protrandric *i.e.* limpets first mature as males and later on change their sex at a certain stage of life history to females. Das and Seshappa (1948), Blackmore (1969), and Thompson (1980) proposed the same hypothesis. Many other limpet species were placed in this category viz. *Acmaea fragitis*, *Patella coerulea*, *Lottia gigantea*, *Notoacmea petterdi* and *Patella aspera*. However, the only species where protoandry has been confirmed is in *Patella oculus* (Branch, 1974a). Rao (1973), in his studies on *C. radiata* of the Waltair coast, could not record any significant difference between sexes. No sexual size differences could also be observed in *Nacella concinna* (Picken, 1980) and *Patella depressa* (Orton & Southward, 1961).

3.8.3 REPRODUCTIVE BEHAVIOR

The sex ratio recorded at Anjuna was 1:1. Results obtained on the variation in the gonadal index suggest that the limpet spawns throughout the year. Results also indicate that spawning activity is reduced during the monsoon period.

During spawning observed in the laboratory, no clustering or pairing of sexes was noticed. Pairing during spawning has been reported in other patellid limpets such as *Patella coerulea*, *P. lusitanica* and in *Patina pellucida* (Fretter & Graham, 1962). Picken (1980) reported a unique spawning behaviour in *Nacella concinna*. During the spawning period, he observed that mature individuals aggregated into temporary stacks of two to six animals, one on top of the other, with no specific order and each stack included males and females. In studies carried out along the Waltair coast, Rao (1973) could not observe any semblance of pairing in *C. radiata*.

During spawning, the gametes were shed freely into the water as in all other patellid limpets. What exactly triggered off the spawning in the laboratory is not clear. One of the plausible factors could have been a change in sea water temperature. As can be seen from Table 2, the maximum range in mean minimum and maximum air temperatures are recorded in December-January. In the laboratory, the temperature of the water in the tanks wherein the limpets were placed depends on the ambient air temperature. Variations in the temperature of the sea water in the tank could have thus stimulated the limpets to spawn.

The spawning stimulus in littoral limpets has been ascribed to stimulation by wave action (Orton *et. al.*, 1956) or changes in temperature (Fritchman, 1962). Orton *et. al.* (1956) and Orton and Southward (1961) found that high winds induced spawning in *Patella vulgata* and *P. depressa*. They observed that strong onshore winds resulted in rough seas, the effect of which is maximal during the low tide period and acted as a mechanical trigger in stimulating spawning in these limpets. Rao (1975a) observed that peak spawning periods of *C. radiata* along the eastern coast coincided with the high winds associated with the southwest and northeast monsoons.

Nacella concinna an Antartic littoral species spawns in the Austral spring and summer, due to a rise in sea temperature (Picken, 1980). Shabica (1971) had ealier observed that a change in temperature was responsible for the final maturation of gametes in *N. concinna*. The importance of temperature and salinity in inducing spawning in different species of animals is well known. An increase in temperature in the scallop *Aquipecten irradians* (Sastry, 1966), decrease in salinity for *Stomopneustes variolaris* (Giese *et. al.*, 1964) and changes in salinity in *Holothuria scabra* (Krishnaswamy & Krishnan, 1967) were all found to induce spawning. Struhsaker (1966) while studying the breeding and spawning in the Hawaiian *Littorina* sp. observed that although temperature probably does not inducc spawning, extreme temperatures may suppress it.

3.8.4 FEEDING BEHAVIOR

In some limpets such as *Acmaea pelta* (Craig, 1968) and *Patella vulgata* (Hartnoll & Wright, 1977), movement and feeding are regarded as two separate activities. However, *C. radiata* feeds as it moves. Laboratory observations in glass tanks in the laboratory showed the mouth and radulae in constant and continuous motion as the limpets moved when submerged under water, suggesting that movement and feeding are interlinked activities. Perhaps the entire course of movement corresponds completely with feeding activity. Based on observations of radula rasping, Little and Sterling (1985) reported that the activity periods of *Patella vulgata* while away from the home scar were exclusively concerned with feeding. Chelazzi *et. al.* (1994a) in their studies on *Patella vulgata* using motorgraphic and sonographic recordings observed that rasping began 1-2 hrs before leaving home and occured during the whole period spent away from home thus suggesting that movement activity was correlated with feeding.

C. radiata is a herbivorous grazer feeding primarily on diatoms and supplemented by other macroalgae like *Enteromorpha* spp. and *Chaetomorpha* sp.. The diet of the limpets reflected the availability of algal species at Anjuna. It can thus be considered as a generalist grazer. The algal flora at Anjuna has been widely studied (Untawale & Dhargalkar, 1975; Agadi, 1986; Acharya, 1989; Mehtab, 1994). *Chaetomorpha* sp. was recorded in the gut of limpets in significant quantities (19%) in October (Table 6). Mehtab (1994) reported that at Anjuna, this algal species begins growing in October and is scarce in March. Most limpets are generalist grazers feeding on any microflora or detritus available on the rock faces (Branch, 1971; Simpson, 1976; Creese, 1978) but there are some species which feed on specific macroalgae. A compilation of published reports on the diets of herbivorous marine prosobranch gastropods is available (Steneck & Watling, 1982).

3.8.5 MOVEMENT PATTERNS

The daily displacement rate of *C. radiata* was 25.3cm/day in February and 40.5cm/day in May. Most excursions recorded in May were short, less than 28cm from the base (Fig. 36). These results are comparable with those obtained for other limpets.

Becket (1968) reported average daily distances ranging from 16.3cm to.40.6cm in *C. ornata* and *C. radians* respectively. Underwood (1977) reported a mean distance of 42cm/day for the non homing limpet, *C. tramoserica*.

Observations recorded in the field in the present study indicate that *C. radiata* is active only during the flood tide, independent of the time of the day and that activity ceases during exposure. Movements begin with the splashes of the incoming tide. Thus, activity in *C. radiata* is initiated by the stimulus provided by the incoming tide. Rao and Ganapati (1971a) also observed activity in *C. radiata* only during flood tide. Villee and Groody (1940) observed no movements in large individuals of *C. digitalis* and *C. scabra* during low tide, only smaller individuals of both species moved during high tides in the daytime. Galbraith (1965) observed *Lottia gigantea* and *C. digitalis* to remain still when dry and exposed. White (1968) observed that *C. scabra* moved when submerged or amidst heavy wave action. Miller (1968) reported that *C. digitalis* was active both during the day and night during high tide and inactive during low tides. Breen (1971), however, observed *C. digitalis* to be in their shelter sites during the day high tides. Collins (1978) observed *C. digitalis* and *C. scabra* moving during night low tides. Beckett (1968) observed movement of *C. radians* and *C. ornata* when submerged and also on moist rock surfaces at night. On the other hand, Hirano (1979) observed *C. toreuma* to be highly active as the low and high tide commenced, regardless of the time of the day, and activity reduced during complete emersion and submersion. These reports support observations that activity in limpets is stimulated by the splash and waves of incoming tides.

One important field observation that was noted was that each excursion ended up in the limpets orienting themselves in a slightly different angle. It was also observed that limpets never retraced their paths on succeeding excursions, suggesting that their movements were non-random or selective. This might therefore enable them to avoid areas previously grazed resulting in an efficient exploitation of grazing areas. Field evidence for the non-random movements in patellid limpets have been reported by Beckett (1968). Cook and Cook (1978), in their studies on two pulmonate limpets, reported the avoidance of previously grazed areas only when the time gap between excursions exceeded 4 hrs. They suggested that ephemeral clues, such as the position of the sun, could help limpets identify previously grazed areas but the evidence is lacking. In another study, though limpets were observed to head for random directions, a slight avoidance of previously grazed areas by *P. rustica* has been reported (Chelazzi *et. al.*, 1994b). Earlier, Cook (1970) reported that siphonariid limpets could detect mucous trails for upto 48h in the laboratory. It is possible, though not established, that *C. radiata* also uses mucous trails as clues to avoid grazed areas. Although it is known that limpets are able to recognize previously grazed areas, the mechanism is not clearly understood.

Another noteworty field observation was homing. The subsequent return of each limpet to the original place indicates that *C. radiata* was homing during that part of the year. It must be noted that the movement patterns carried out in this study pertains to limpets inhabiting the upper and mid shore and it is thus not known whether lower shore limpets also home. Moreover, homing was only observed in May. Field observations on the movement pattern of limpets in February did not suggest any homing behavior. Thus, *C. radiata* can be considered as a temporary homer. Rao and Ganapati (1971a) observed homing in *C. radiata* only on rough surfaces; chances of homing on smooth surfaces being very low. The homing activity of limpets and the different factors responsible for it are reviewed in Branch (1981).

Homing, in general, has been considered as an adaptation against desiccation during low tide (Breen, 1971) and to reduce vulnerability to dislodgement by wave action (Orton, 1929; Test, 1945). This could perhaps explain why limpets homed in May and not in February. Maximum temperature at Anjuna was recorded in May; in February, temperature was lower (Fig. 4). Thus, homing in May could be an adaptation against desiccation. Along the intertidal rocky shore of Jordan, *C. radiata* was also observed to be a temporary homer (Hulings, 1985). More detailed studies are however required to ascertain the implications and modality of homing.

CHAPTER IV

POPULATION STUDIES

4.1 POPULATION STRUCTURE

Mean monthly densities of the limpet, *C. radiata* at Anjuna are presented in Fig. 38. It can be seen that the densities varied from month to month, with maximum densities recorded during the pre-monsoon and post-monsoon seasons: in October '93 (14.7/m^2) and September '94 (13.4/m^2) and in February '94 (10.0/m^2). Density of limpets in October '94 was however very low. Low densities were recorded during the monsoon period.

In order to determine the population structure, frequency histograms of shell lengths of *C. radiata* recorded in the field were constructed for each month and the shifts in modal peaks of statistically fitted Gaussian curves analysed. Figure 39 to Fig. 41 illustrates the size frequency distribution of the natural population of limpets at Anjuna from September '93 to October '94. It can be seen that limpets of shell length less than 14mm are not well represented in the frequency histograms. Smaller sized individuals were recorded in September, December and March. Only one modal group could be observed in August '94.

The resulting frequency histograms exhibited modal peaks which were not very well defined. Attempts were made to

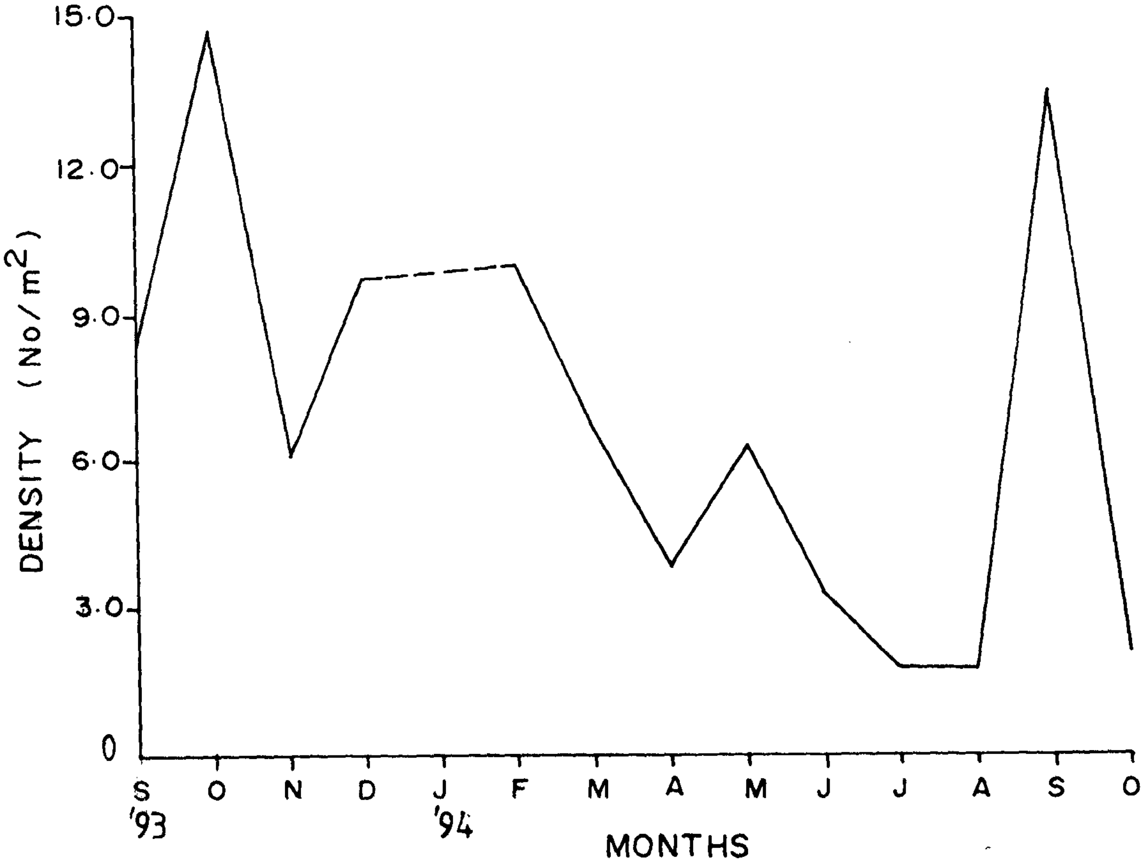


Fig. 38 The monthly variations in the density of *C. radiata*.

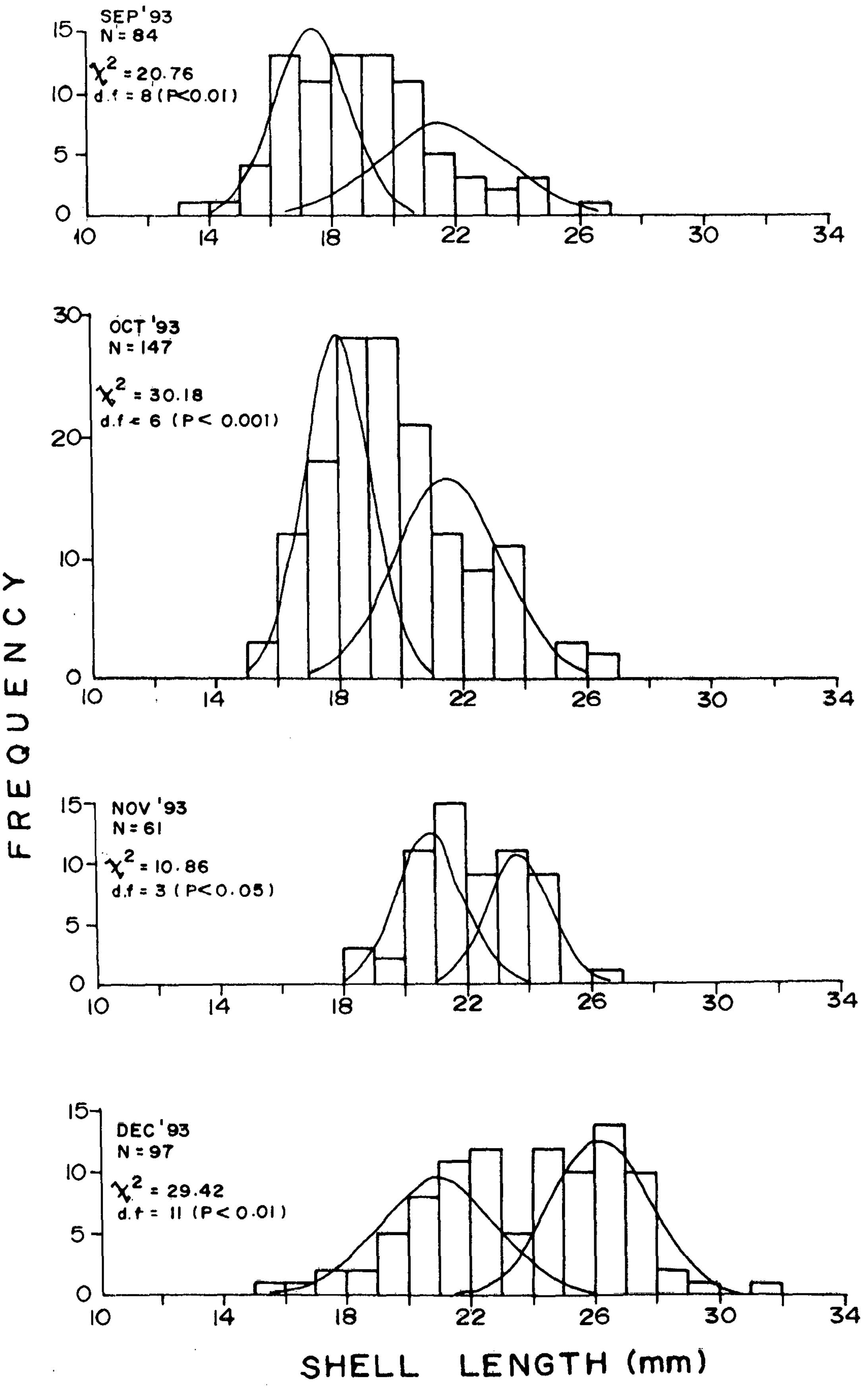


Fig. 39. Normal curves superimposed on the size frequency histograms of the limpet population from September '93 to October '94. (N = number of limpets).

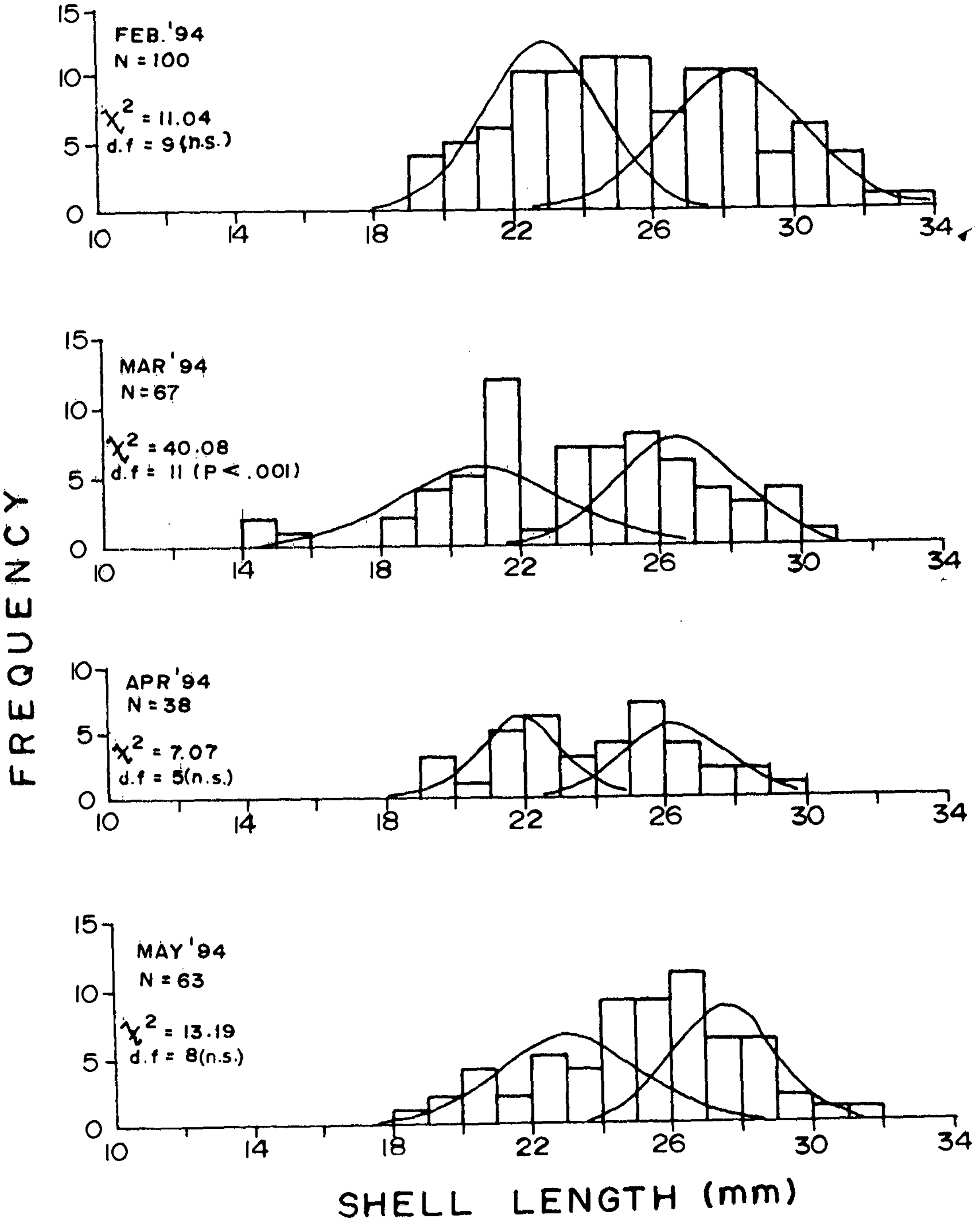


Fig. 40. Normal curves superimposed on the size frequency histograms of the limpet population from September '93 to October '94. (N = number of limpets).

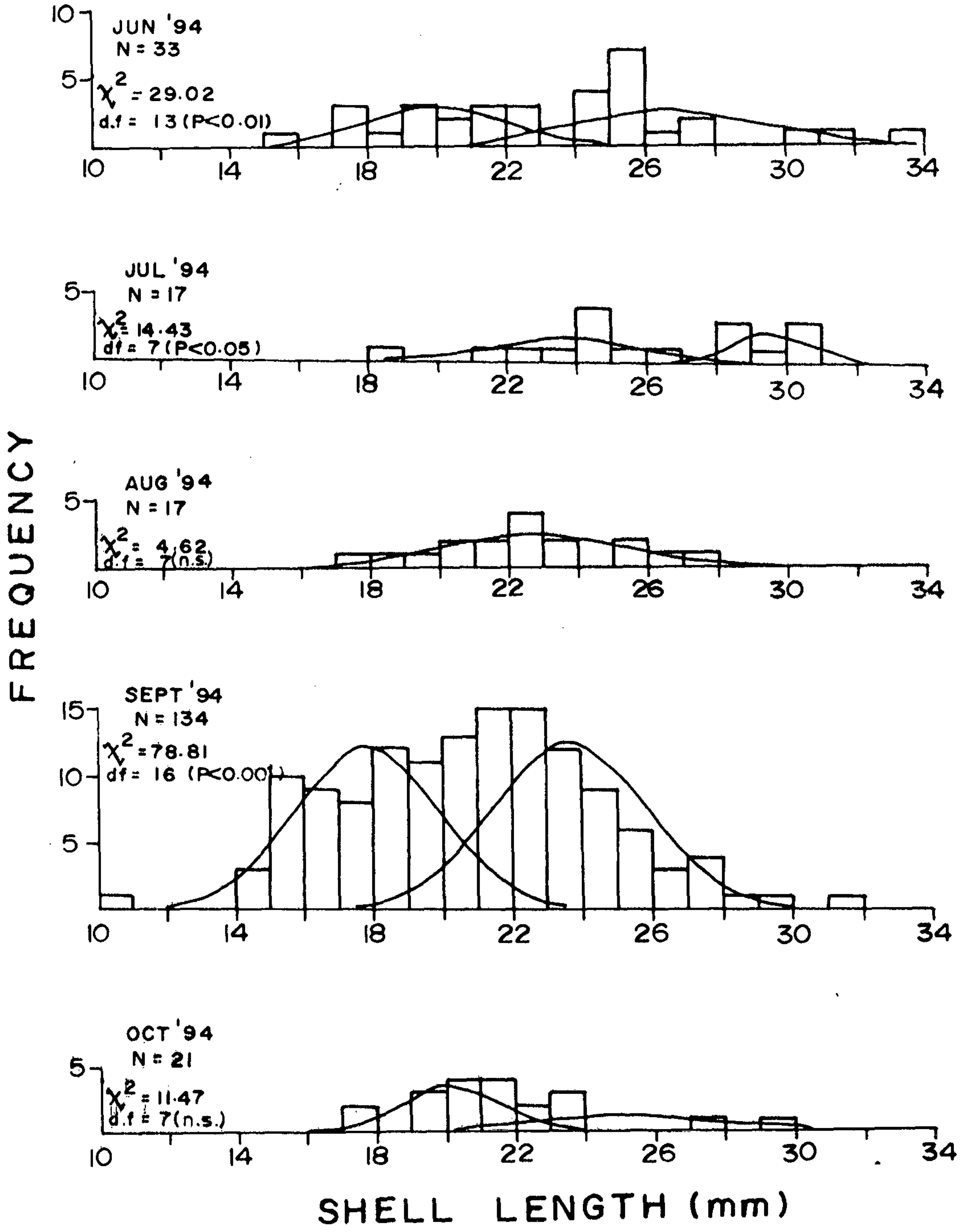


Fig. 41. Normal curves superimposed on the size frequency histograms of the limpet population from September '93 to October '94. (N = number of limpets)

statistically separate the polymodal frequency distribution into their component Gaussian curves representing various age groups, but only two normal curves, sometimes one, could be reasonably fitted to the data (Fig. 39 to Fig. 41).

Shifts in the peaks of modal shell length could be observed. Taking into account the frequency size distribution of all limpets during the study and the statistical fit of normal curves, four population groups of limpets could be distinguished and their growth pattern followed. One population group could be observed from September '93 to February '94. The growth of the second group could be followed upto July '94. The third population group was observed from March '94 upto October '94 while the fourth group made its appearance in September '94.

For the sake of clarity, the mean shell length and their 95% confidence limits, extracted from Fig. 39 to 41, are plotted in Fig. 42. It can be seen that group A shows a clear shift in modal shell length from September '93 upto February '94. The mean size of this group increased from 21.52mm in September '93 to 28.38mm in February '94. The growth of group B limpets could be traced from September '93 upto July '94, after which it could not be traced. During this period, the mean shell size increased from 17.31mm to 29.5mm. During September and December '93 smaller size classes of limpets were recorded, which apparently masked the mean size of group B. The growth of group C, apparent in March '94 could be followed upto the end of the sampling period. These limpets grew from a mean shell length

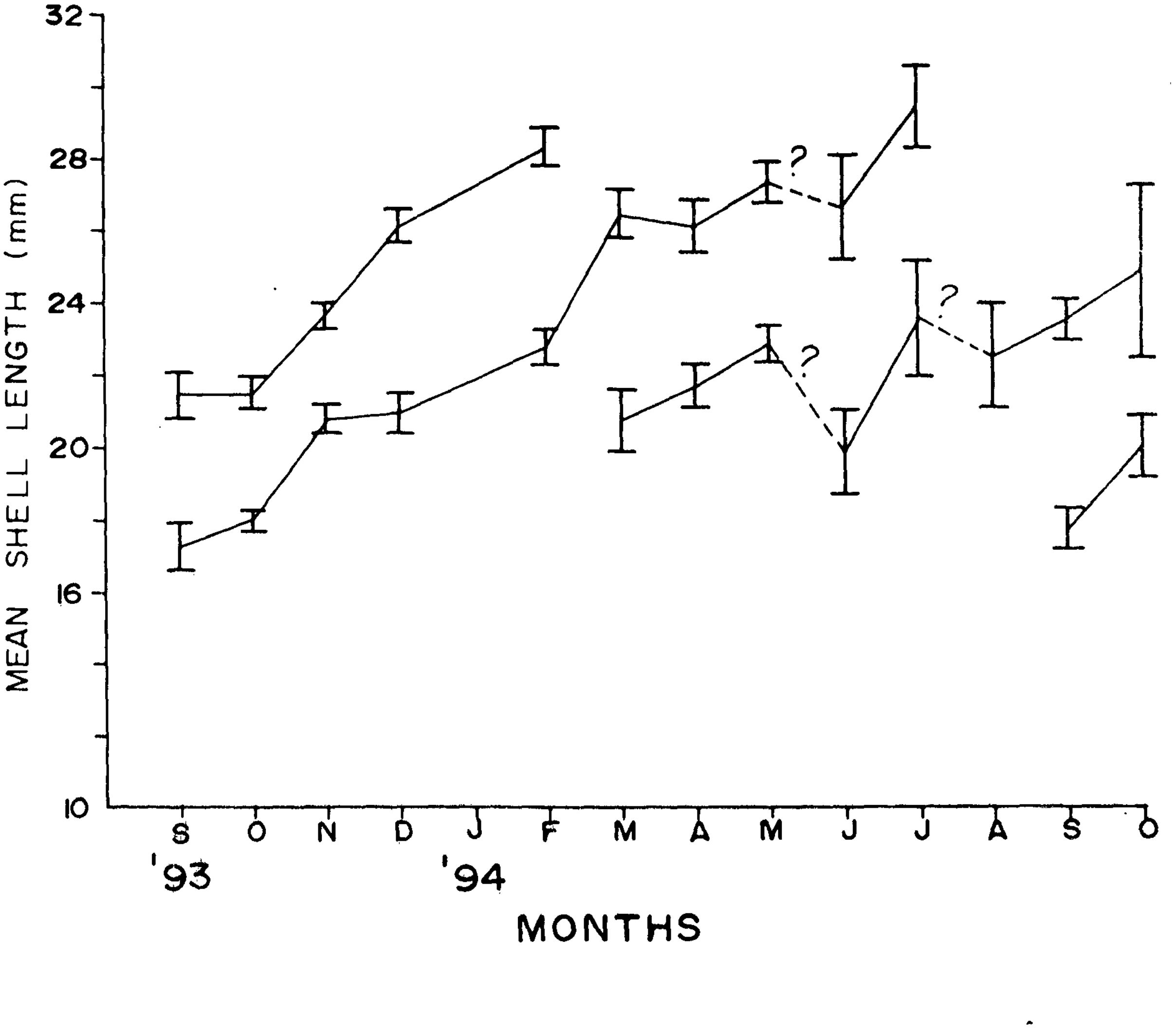


Fig. 42. Monthly variations in the mean shell length (± S.E.) of the different groups of the limpet population from September '93 to October '94.

of 20.70mm upto 24.95mm. A new group D, as evidenced by the presence of smaller sized limpets, appeared in September '94. This population group increased in shell length from 17.78mm in September '94 to 20.08mm in October '94. In group B and C, there was sometimes an apparent decrease in mean shell length as indicated by the broken lines.

Small limpets grew faster than larger limpets. It can be seen that the growth rate, inferred from monthly increase in shell length, was relatively high from December '93 to March '94. No other particular trend could be observed. The approximate mean growth rate during the pre-monsoon, monsoon and post-monsoon seasons was 1.32mm/month, 1.22mm/month and 1.60mm/month respectively. The mean shell length as well as the number of individuals comprising each group of the population are given in Table 7. It can be seen that the population size of the groups, which ought to decrease or remain constant, at times increased. These problems highlight the practical difficulties faced in separating polymodal frequency distribution data into component curves.

4.2 ESTIMATION OF GROWTH BY TAGGING

Information required to understand the population dynamics can also be obtained by tagging individual organisms. A considerable amount of time was spent experimenting with different glues to select a suitable adhesive which would

TABLE 7

Mean shell length of different groups of the population of *C. radiata* from Sept. '93 - Oct. '94 (n=number of limpets.).

	GROUPS			
MONTHS	A	B	C	D
September'93	21.52 (n=38)	17.81 (n=46)		
October	21.55 (n=71)	18.00 (n=76)		
November	23.69 (n=27)	20.84 (n=34)		
December	26.19 (n=51)	20.94 (n=46)		
February '94	28.38 (n=49)	22.85 (n=51)		
March		26.40 (n=34)	20.70 (n=33)	
April		26.18 (n=20)	21.73 (n=18)	
May		27.40 (n=31)	22.96 (n=32)	
June		26.69 (n=17)	19.93 (n=16)	
July		29.50 (n=07)	23.59 (n=10)	
August			22.54 (n=17)	
September			23.60 (n=70)	17.78 (n=64)
October			24.95 (n=08)	20.08 (n=13)

withstand the rigours of the nature. The difficulty was compounded because it was intended to track individual limpets. Out of 947 limpets marked, only 190 (20%) of them could be observed on subsequent field visits. Of these 190 limpets, only 112 (59%) could be observed subsequently. One of the individual limpets marked on 2-10-1993 could be recovered on 20-4-94, *i.e.* after 200 days. Marked limpets sometimes migrated out of the study area and some, not all, returned subsequently, after a period of 41-200 days. Some marked limpets were found amidst boulders, adjacent to the study area. During the monsoon season, when wave action is intense, most limpets were restricted to protected areas or perhaps migrated out of the study area to safer areas among the rocky boulders.

Data on the shell length of marked limpets was used to study its growth. In the von Bertlanffy growth model, three parameters need to be estimated: L_∞, the asymptotic shell length, K, the growth constant and t_0, the theoretical age of limpets at zero shell length. Since growth is rapid in the early stages, it was reasonable to assume that the value of t_0 was negligible. Similar assumption was made by Rao (1976) in his study on *C. radiata* and by Ward (1967) in his study on *Fissurella barbadensis*. The coefficient of variation of trial values of L_∞ obtained from the Munro plot is shown in Fig. 43. The optimal value of L_∞ was 39.41mm with a K value of 0.089. The estimated value of L_∞ lies close to the actual size of the largest limpet (36.75mm) recorded in the field.

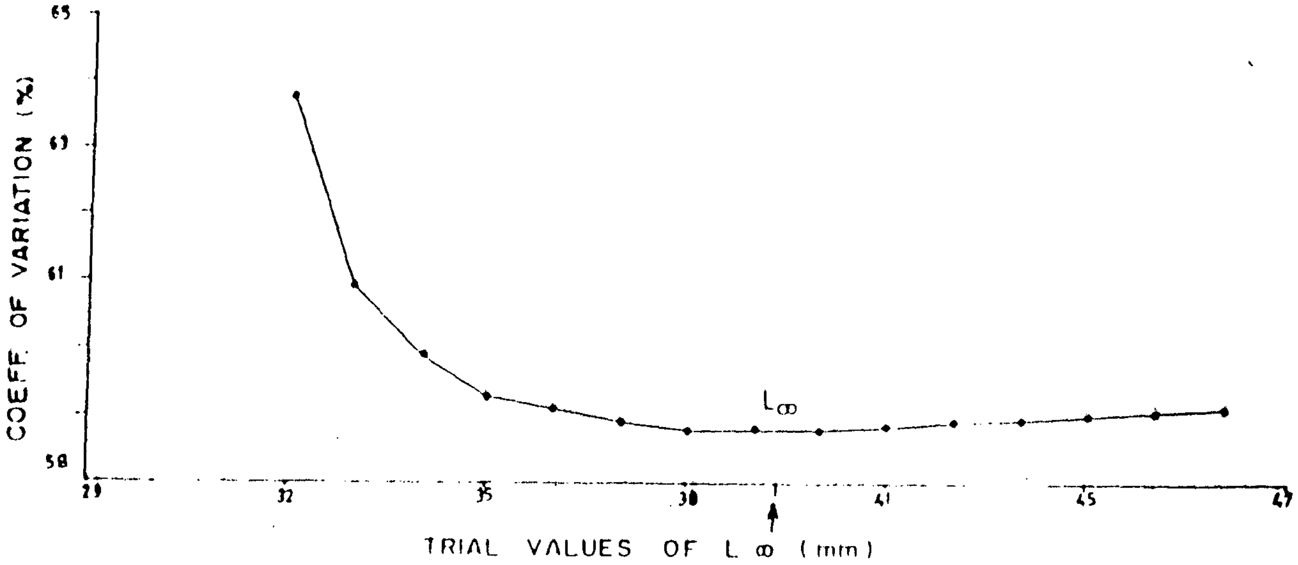


Fig. 43. The coefficient of variation of trial values of L_∞.

The von Bertlanffy growth curve obtained using the estimated parameters is shown in Fig. 44. The age of marked limpets was estimated using the estimated parameters and are superimposed with the curve. Data obtained in the laboratory on the age and growth of juvenile limpets are also plotted. It can be seen that observed growth of the limpet follows the von Bertlanffy growth model.

The growth curve of *C. radiata* is asymptotic. The limpet attains a shell length of 25mm after the first year and subsequently a shell length of 34.72mm, 37.79mm, 38.85mm and 39.41mm in the second, third, fourth and fifth year respectively. The size when the limpet attains sexual maturity would correspond to age between 3 to 5 months. The theoretical estimated longevity is around 5 years.

Data obtained from tagged limpets was also used to estimate seasonal growth rates using the 'forced' Gulland and Holt plot (Fig. 45). L_∞ value was obtained earlier using the Munro plot. The growth constant, K, during October to January (post-monsoon) was 0.11; 0.09 during February to May (pre-monsoon) and 0.07 during June to September (monsoon). The seasonal growth rates were 1.32mm/month, 1.05mm/month and 1.94mm/month for the pre-monsoon, monsoon and post-monsoon seasons respectively. The mean growth rate estimated by pooling the data obtained during the entire study period was 1.34mm/month.

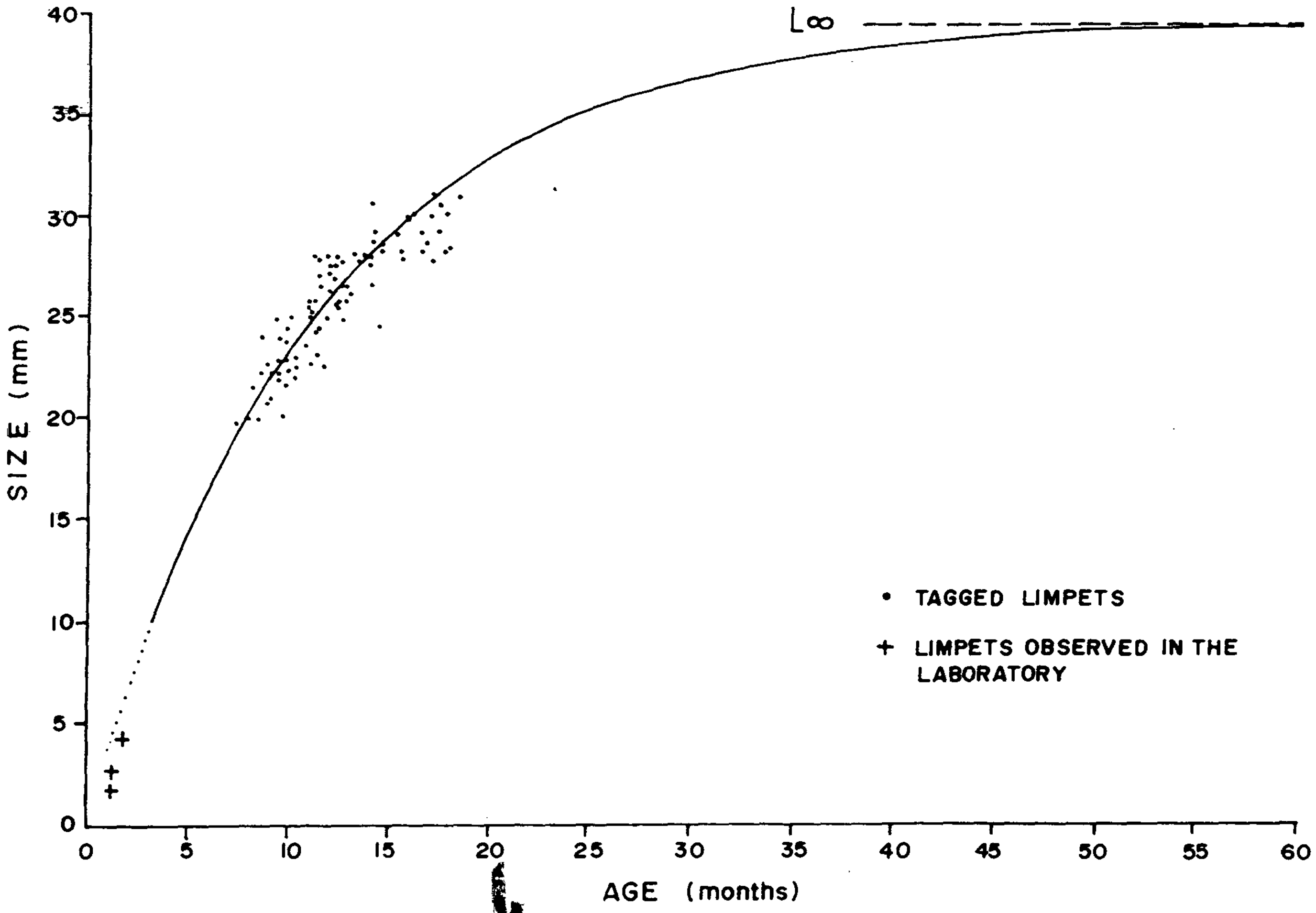


Fig. 44. The von Bertlanffy curve showing the size attained at specific ages.

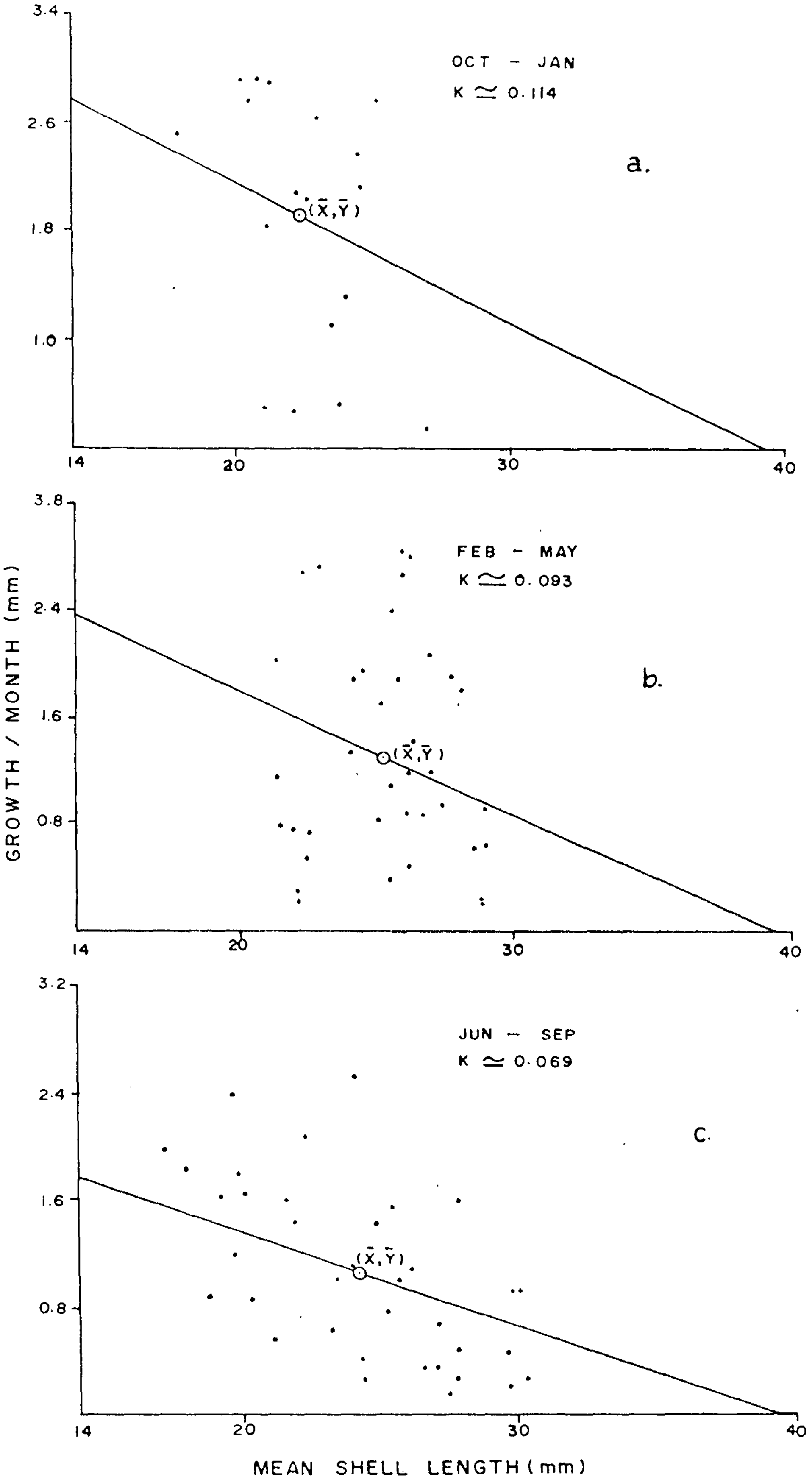


Fig. 45. The seasonal variations in the growth rates of *C. radiata*. Post-monsoon (a) Pre-monsoon (b) Monsoon (c).

4.3 DISCUSSION

4.3.1 POPULATION STRUCTURE

One of the pre-requisites for the study of the population dynamics or population structure of any organism is the age of the organism. As the size of organisms is related to its age, many ecologists have been analysing the polymodal frequency distribution of sizes of the population of organisms with time in order to follow the dynamics' of the population. Harding (1949) and later, Cassie (1954) used probability paper to analyse the component Gaussian curves. Taylor (1965) also suggested a technique for analysing such data. These methods have been widely employed wherever the age groups of the organism had to be delineated.

In the present study, the statistical fitting of Gaussian curves was employed to separate age groups and its goodness of fit tested. The results obtained confirmed some of the practical problems encountered, such as the separation of distinct size classes representing age groups. As the limpet, *C. radiata*, breeds and grows throughout the year, well defined size groups were not formed. Similar observations were made by Ward (1967) while studying the distribution of the keyhole limpet, *Fissurella barbadensis* in the West Indies and by Rao (1976) in his study of *C. radiata* at Waltair, on the east coast of India. Rao (1976) observed about 2 modal groups but could trace the fate of only one of them. Older limpets could not be successfully statistically separated into separate age groups because of their asymptotic growth. resulting in the merger of their size groups.

Analysis of the frequency distribution revealed the presence of at least four groups and their shift in modal peak as well as growth could be reasonably followed. The goodness of fit of the Gaussian curves were in some cases not significant, highlighting the difficulties in analysing the data. The number of individuals in each group varied from month to month and in some cases increased. indicating that the population was complex and could possibly further comprise of a number of sub groups. Attempts to statistically separate these sub groups were futile. Further, the density of limpets varied from month to month. Observations on marked limpets suggested that limpets migrated out and into the study area. Thus the low densities recorded during the monsoon period could perhaps be ascribed to migration. During this period only a few limpets of the different size groups remained in the study area.

The non observation of limpets less than 10mm in shell length during this study implies that either they were missed or they were inaccessibly located in the narrow fissures and crevices of the study area.

The largest number of small sized limpets were recorded in September '94. From the von Bertlanffy growth curve, these limpets can be assumed to have been born in March-April '95.

Similarly, the juvenile limpets recorded in December '93 and March '94 could be assumed to have been born in July '93 and October '93 respectively. These observations reaffirm that *C. radiata* is a continuous breeder.

4.3.2 GROWTH

Tagging has been used to follow the growth of limpets by several investigators. Marking methods employed ranged from marking the shell using enamel paint (Rao, 1976), filing marks on shells (Magruder & Kay, 1983; Fletcher, 1984a) to the elaborate sticking of numbered tags (Branch, 1974b; Phillips, 1981). The last two methods enables monitoring of individual limpets. In a study carried out at Waltair, Rao (1976) marked 60 limpets using common enamel paint marks for a number of limpets of similar shell size and monitored their growth for four months, remarking them whenever necessary. The percentage recovery of marked limpets (20%) was similar to that obtained in the present study. The low recovery percentage necessitates marking of a large number of limpets, a laborious process. Nevertheless, results obtained from tagged individuals are much more accurate.

The growth of *C. radiata* measured as changes in the shell length varied with the limpets age. Smaller limpets grew faster than larger ones. There were slight variations in the seasonal growth rates. Both methods of estimating growth (analysis of size frequency histograms and tagging) yielded roughly the same results. Growth is rapid in the early stages, sharply declining after the first year. The decline in growth rate could possibly indicate increased allocation of energy for reproduction. The curve attains the asymptote after the third year.

Though the theoretical life span of the limpet, when the limpet attains the asymptotic shell length, was estimated to be 5 years, the maximum size of limpets in the field was not more than 34mm suggesting that they survive in the field for about two years. The cause of mortality could be due to the presence of predators. Besides crows, crabs (*Grapsus* sp.) and molluscs (*Euplica versicolor*, *Gyraneum natator*, *Conus planorbis*) are the likely predators of limpets. These moluscs were however not abundant and no observations were recorded in the field. During field visits, it was also observed that some of the limpets were being collected for human consumption.

The growth curve of *C. radiata* inhabiting the rocky shores of Waltair, along the eastern coast of India, was different. Seasonal variations in growth rates were not observed, probably because marking was carried out for a few months only, and ascribed to the absence of marked climatic variations (Rao, 1976). Further, they attained a length of 20mm at the end of the first year, 30mm at the end of the second year, 36mm at the end of the third year and 39mm at the end of the fourth year. Their asymptotic shell length, L_∞, was 42.55mm, growth constant, K, 0.05434, mean monthly growth rate 1.16mm, theoretical life span, 8 years and they were presumed to survive for 3 years. Thus, when compared to *C. radiata* at Anjuna, they exhibit a slower growth rate, a longer theoretical life span but a longer survival period in the field and a larger asymptotic shell length.

Limpets have variable growth rates depending upon a multitude of factors. Several investigators have related growth rates with food availability (Blackmore, 1969; Sutherland, 1970; Phillips, 1981; Parry, 1982a). *Patella cochlear*, *P. granatina*, *P. granularia* and *P. oculus* attain a first year length of 22mm, 35mm, 18mm and 56mm respectively (Branch, 1974b). These differences in growth rates have been partly attributed to the nutritive value of different food sources. In *Siphonaria diemenensis*, growth rates vary and food availability has been reported to be the major determinant of variation of not only of its growth but also of its survival (Quinn, 1988a).

At Anjuna, analysis of the gut contents of *C. radiata* revealed that its diet could be related to the abundance of algae in the study area. The limpet could be considered as a generalist grazer and not a species specific grazer. The presence of other grazers is likely to increase interspecific competition thereby restricting the area available for feeding. The dominant grazers at Anjuna are prosobranch such as littorinids (*Littorina* spp., *Nodilittorina* spp.), neritids (*Nerita chamaeleon*, *Nerita albicilla*), *Trochus stellatus*, *Turbo intercostalis*, *Euchelus quadricarinata*, *Planaxis sulcatus* and *Ochetoclava sinensis* (Coutinho, 1993). There are however no studies on the competition amongst these grazers at Anjuna.

Observations revealed that the limpet wandered for longer distances, as indicated by the mean daily displacements, and homed during the hot season. Wandering would enable the limpets to explore larger areas for grazing. At Anjuna, algal growth begins in September with peak growth in February - March and minimal growth during the monsoon season (Dhargalkar, 1981). Limpets being grazers might also be affected by this seasonal trend in food availabilty. Thus, this would imply that the growth rate would be higher during the pre-monsoon season. This was however not the case. On the other hand, consideration of physical factors prevailing during the seasons could perhaps explain this apparent anomaly. During the pre-monsoon season, the overall mean environmental temperature rises resulting in a higher metabolic activity. Further, during this season, the low tide periods occur in the middle of the day, when temperatures are high resulting in increased metabolic activities. Such increased energy utilization might therefore reduce energy apportionment for growth. Field observations revealed that *C. radiata* homed during this season. Homing, as an adaptation to withstand desiccation stress, enables the limpets to conserve energy.

Quinn and Brown (1988) have related growth rates to wave action. Increased wave action reduces foraging time. Increased wave action would force the animals to adhere firmly to the substratum to prevent dislodgement. Thus energy that could be utilized for growth would then be expended on countering physical stress. Thompson (1980), observed that with intensification of wave action ,the ratios of *P. vulgata* to *P. aspera* numbers and growth declines. Branch (1981) attributes these differences to the increased oxygen consumption in the animals that are forced to adhere tightly to the substratum resulting in increased energy losses. Lower growth rates observed in the study area during the monsoon season could thus be not only because of shortage of food but also because of increased metabolic activity.

4.3.3 LIFE HISTORY TRAITS

Shorter life span, faster growth and precocious maturity are some of the life history traits generally associated with the tropical species (Naylor, 1965). The limpet, *C. radiata*, in this study conforms with these traits. The life span of the limpet at Anjuna was estimated to be about 2 years. Along the east coast of India, this limpet is reported to live for approximately 3 years (Rao, 1976). The life span of *Cellana exarata* and *C. sandwicensis* along the Hawaiian coast is reported to be around 1.5 years (Magruder & Kay, 1983). In sharp contrast, *Patella vulgata* survives for about 3 to 15 years along the temperate British coasts (Fretter & Graham, 1962).

Growth of limpets is also faster in tropical regions. At Anjuna, *C. radiata* attains a shell length of 25mm in the first year. At Waltair, it grows to 20mm during the same period. *Fissurella barbadensis* from the West Indies is 26.5mm in length at the end of one year (Ward,1967). The two species of Hawaiian patellid limpets *viz. Cellana exarata* and *C. sandwicensis* attain a shell length of 40mm after the first year (Magruder & Kay, 1983). Most temperate limpets, however, grow at a comparatively slower rate. *Patella vulgata* grows to a length of 9mm in one year (Lewis & Bowman, 1975). *Acmaea scabra* is only 2mm-6mm at the end of one year (Sutherland, 1970). There are however exceptions. *Patella oculus* attains a shell length of 55mm in one year (Branch, 1974b). Orton (1928) reported a maximum size of 35mm for one year old *Patella vulgata*.

Early sexual maturity and intensive breeding has been reported in limpets of tropical regions. At Waltair, *C. radiata* attains sexual maturity when 6-8 months old and measures 10-15mm in shell length and breeds continuously (Rao, 1973, 1976). At Anjuna too, observations suggest that the limpet attains sexual maturity when 10-15mm in size (3 to 5 months old). The Hawaiian patellid limpets attain sexual maturity when 4-5 months old (Magruder & Kay, 1983). The temperate limpet, *Patella vulgata*, however attains sexual maturity only when one year old, when they are about 20mm in length.

Many investigators have obtained a striking inverse correlation between the growth coefficient, K, and longevity. This has been particularly true in the case of *Patella vulgata* inhabiting different localities (Choque, 1968; Lewis & Bowman, 1975; Thompson, 1979, 1980; Branch, 1981). In contrast to the fast growing species discussed earlier, there are also slow growing species like the Antarctic limpet, *Nacella concinna*, which has a low K value (0.07), a low metabolic rate, sexually matures after 7-8 years, and has a prolonged longevity (30 years) probably as an adaptation to the low availability of food (Picken, 1980). In South Africa, *P. longicosta* and *P. cochlear* too are slow growing species having a longevity of approximately 12-17 and 15-25 years respectively (Branch, 1974b).

An exception to this hypothesis is the observations by Sutherland (1970) that though high shore *Collisella scabra* grew faster than low shore individuals, they suffered a lower mortality and lived longer. Creese (1981), in his studies on some species of limpets in New South Wales reported the growth pattern of two patellid species *Patelloida latistrigata* and *P. alticostata*: the former grew slowly, attained a size of 15.1mm but had a longevity of only 3 years while the latter grew faster, attained a size of 22.3mm and had a longevity of 5-6 years. He explained that *P. latistrigata* lives in close association with barnacles which may limit the maximum size to which it can grow.

Branch (1981), reviewing this relationship, suggests that the life expectancy would shorten with rapid growth and early sexual maturity as these traits would exhaust energy reserves. In addition, these may also reduce energy available for defensive structures thus enhancing mortality risks. He concluded that although growth pattern may be flexible, different species display different patterns as adaptations to particular circumstances.

CHAPTER V

ENERGY BUDGET

5.1 COMPONENTS OF ENERGY FLOW

The energy budget of a population has been standardized by the International Biological Programme (Petrusewicz, 1967) and is summarized by the following equation:

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

where C is the energy content of food consumed, P is the total energy produced as flesh, secretions or gametes, R is the energy lost due to metabolism, F is the energy thrown out as faeces and U is the energy lost through urine and other exudates. Conventionally, as it is impractical to measure metabolic heat loss directly by direct calorimetry, oxygen consumption is measured and converted into heat output to represent energy lost through metabolism (R).

The total energy utilized for production, P, can be further partitioned into several components. In limpets, as mucus secretion could be important, the energy budget can be rewritten as:

$$C = P_g + P_{rep} + P_{mucus} + R + F + U \qquad \text{(Branch, 1981)}$$

where *Pg*, *Prep* and *Pmucus* is the energy channelled into somatic growth, reproduction and mucus production respectively. The energy allocated for somatic growth and recruitment, *Pg*, is the sum of any net change in the energy content of the standing stock (Δ B) and that of individuals eliminated from the population through mortality, also referred to as elimination. The energy allocated for reproduction, *Prep*, comprises of energy utilized for gonad growth (*Pr*) and spawned gametes (*Prg*) and are distinguished in the present study.

Mucus production could constitute an important component of the energy budget of limpets as it accounts for almost half of the production in *Patella longicosta* (Branch, 1981). In the present study, attempts were made to quantify the mucus secreted by *C. radiata* placed on glass panes and collecting the mucus from the foot at regular intervals. However, as the amount of mucus secreted by individual limpets not only varied widely but was also inconsistent, the data was discarded as it would not result in meaningful production estimates. Branch and Marsh (1978) have also reported widely varying amounts of mucus secretion. In view of this, *Pmucus* has been ignored in energy budgets of limpets.

The calorie has been the most logical unit to quantify allocation of energy and has been the primary unit of energy measurement for laboratory and field studies (Englemann, 1961). The calorie has now been replaced by the joule (1 calorie = 4.184 joules) as the energy unit. In the present study, the energy content of food consumed (C), the energy used for mucus production (*Pmucus*), the energy thrown out as faeces (F) and the energy lost as urine (U) were not quantified due to practical difficulties involved in their estimation. As available reports on production components of the energy budget sometimes are presented in terms of wet weight and/or dry weight, production estimates in the present study are presented as wet weight, dry weight and calories to facilitate comparisons. Results, along with their 95% confidence limits, are tabulated in Table 8 to Table 10. These values are standardised, to avoid discrepancies arising due to the varying number of days in the intervening period, and are graphically presented in Fig. 46 to Fig. 48. The standardised seasonal values of production estimates are presented in Fig. 49.

5.1.1 TOTAL PRODUCTION

The monthly total production in terms of wet weight, dry weight and calories was highest during September-October '93 with values reading 10.200 g/m^2, 2.470 g/m^2 and 12377 cal/m^2 respectively (Fig. 46 to Fig. 48). Lowest values were recorded in July-August '94 with values reading 0.309 g/m^2, 0.061 g/m^2, 322 cal/m^2 respectively. Total production was highest during the post-monsoon season and lowest during the peak monsoon season (Fig. 48).

The annual total Production/Biomass ratio (P/B) was 0.198, 0.207 and 0.207 in terms of wet weight, dry weight and calories

Table 8. Wet weight production of *C. radiata* at Anjuna (g/m²)

Period	No. of Days	Mean Density (/m²)
Sept.'93 - Oct. '93	28	11.55
Oct. '93 - Nov. '93	28	10.40
Nov. '93 - Dec. '93	19	7.90
Dec. '93 - Feb. '94	83	9.85
Feb. '94 - Mar. '94	23	8.35
Mar. '94 - Apr. '94	32	5.25
Apr. '94 - May '94	41	5.05
May '94 - June '94	17	4.80
June '94 - July '94	35	2.50
July '94 - Aug. '94	30	1.70
Aug. '94 - Sept.'94	29	7.55
Total	365	

Period	Total biomass (g)	Total production
Sept.'93 - Oct. '93	41.010 (36.390 - 46.353)	9.520 (5.984 - 13.964)
Oct. '93 - Nov. '93	36.716 (32.716 - 41.327)	7.567 (4.783 - 11.028)
Nov. '93 - Dec. '93	27.775 (23.936 - 32.426)	2.945 (1.816 - 4.409)
Dec. '93 - Feb. '94	46.753 (34.885 - 63.020)	15.448 (5.414 - 31.426)
Feb. '94 - Mar. '94	32.235 (23.894 - 43.802)	2.913 (1.015 - 5.950)
Mar. '94 - Apr. '94	13.903 (10.601 - 18.319)	1.935 (0.687 - 3.869)
Apr. '94 - May '94	15.471 (11.513 - 20.865)	2.455 (0.851 - 5.025)
May '94 - June '94	11.924 (10.149 - 14.133)	0.907 (0.599 - 1.331)
June '94 - July '94	3.001 (2.544 - 3.577)	0.479 (0.312 - 0.697)
July '94 - Aug. '94	1.822 (1.422 - 2.352)	0.309 (0.193 - 0.482)
Aug. '94 - Sept.'94	17.985 (15.142 - 21.422)	4.712 (3.073 - 6.863)
Total	248.597 (203.193 - 307.597)	49.191 (24.727 - 85.047)

Period	Somatic biomass (g)	Somatic production
Sept.'93 - Oct. '93	29.761 (27.100 - 32.716)	6.611 (4.394 - 9.243)
Oct. '93 - Nov. '93	26.445 (24.245 - 28.863)	5.212 (3.495 - 7.214)
Nov. '93 - Dec. '93	19.687 (17.573 - 22.105)	1.995 (1.313 - 2.808)
Dec. '93 - Feb. '94	34.308 (25.626 - 46.194)	10.185 (2.766 - 22.106)
Feb. '94 - Mar. '94	23.617 (17.523 - 32.061)	1.922 (0.519 - 4.185)
Mar. '94 - Apr. '94	10.291 (7.846 - 13.556)	1.290 (0.355 - 2.752)
Apr. '94 - May '94	11.328 (8.443 - 15.254)	1.608 (0.432 - 3.513)
May '94 - June '94	8.569 (7.665 - 9.582)	0.624 (0.457 - 0.822)
June '94 - July '94	2.157 (1.922 - 2.423)	0.330 (0.240 - 0.435)
July '94 - Aug. '94	1.447 (1.145 - 1.841)	0.253 (0.164 - 0.380)
Aug. '94 - Sept.'94	14.036 (11.981 - 16.523)	3.770 (2.581 - 5.334)
Total	181.647 (151.070 - 221.119)	33.800 (16.716 - 58.792)

Period	Gonad biomass (g)	Gonad production
Sept.'93 - Oct. '93	3.138 (1.988 - 4.558)	1.649 (0.612 - 3.085)
Oct. '93 - Nov. '93	3.422 (2.382 - 4.675)	1.437 (0.581 - 2.581)
Nov. '93 - Dec. '93	3.559 (2.397 - 5.063)	0.661 (0.276 - 1.206)
Dec. '93 - Feb. '94	4.975 (4.018 - 6.140)	1.986 (1.058 - 3.225)
Feb. '94 - Mar. '94	3.439 (2.760 - 4.273)	0.374 (0.199 - 0.611)
Mar. '94 - Apr. '94	1.453 (1.195 - 1.761)	0.245 (0.134 - 0.393)
Apr. '94 - May '94	1.655 (1.337 - 2.041)	0.318 (0.168 - 0.520)
May '94 - June '94	1.751 (1.301 - 2.302)	0.088 (0.010 - 0.189)
June '94 - July '94	0.442 (0.325 - 0.587)	0.046 (0.006 - 0.102)
July '94 - Aug. '94	0.242 (0.147 - 0.385)	0.031 (0.003 - 0.073)
Aug. '94 - Sept.'94	2.755 (2.038 - 3.755)	0.551 (0.146 - 1.150)
Total	26.833 (19.888 - 35.540)	7.386 (3.193 - 13.135)

Period	Gamete biomass (g)	Gamete production
Sept.'93 - Oct. '93	8.111 (7.302 - 9.078)	1.260 (0.978 - 1.639)
Oct. '93 - Nov. '93	6.848 (6.088 - 7.789)	0.918 (0.707 - 1.233)
Nov. '93 - Dec. '93	4.529 (3.966 - 5.258)	0.289 (0.227 - 0.395)
Dec. '93 - Feb. '94	7.470 (5.241 - 10.687)	3.277 (1.590 - 6.095)
Feb. '94 - Mar. '94	5.179 (3.611 - 7.468)	0.617 (0.297 - 1.154)
Mar. '94 - Apr. '94	2.159 (1.560 - 3.001)	0.400 (0.198 - 0.724)
Apr. '94 - May '94	2.487 (1.734 - 3.570)	0.529 (0.251 - 0.992)
May '94 - June '94	1.604 (1.183 - 2.249)	0.195 (0.132 - 0.320)
June '94 - July '94	0.402 (0.297 - 0.567)	0.103 (0.066 - 0.160)
July '94 - Aug. '94	0.133 (0.130 - 0.126)	0.025 (0.026 - 0.029)
Aug. '94 - Sept.'94	1.131 (1.122 - 1.142)	0.348 (0.346 - 0.379)
Total	40.054 (32.234 - 50.936)	7.961 (4.818 - 13.120)

Table 9. Dry weight production of *C. radiata* at Anjuna (g/m²)

Period	No. of Days	Mean Density (/m²)
Sept.'93 - Oct. '93	28	11.55
Oct. '93 - Nov. '93	28	10.40
Nov. '93 - Dec. '93	19	7.90
Dec. '93 - Feb. '94	83	9.85
Feb. '94 - Mar. '94	23	8.35
Mar. '94 - Apr. '94	32	5.25
Apr. '94 - May '94	41	5.05
May '94 - June '94	17	4.80
June '94 - July '94	35	2.50
July '94 - Aug. '94	30	1.70
Aug. '94 - Sept.'94	29	7.55
Total	365	

Period	Total biomass (g)	Total production
Sept.'93 - Oct. '93	9.681 (8.577 - 10.980)	2.305 (1.493 - 3.354)
Oct. '93 - Nov. '93	8.706 (7.735 - 9.848)	1.838 (1.198 - 2.664)
Nov. '93 - Dec. '93	6.645 (5.715 - 7.797)	0.720 (0.456 - 1.075)
Dec. '93 - Feb. '94	9.428 (7.543 - 11.900)	3.510 (1.892 - 5.877)
Feb. '94 - Mar. '94	6.512 (5.183 - 8.271)	0.663 (0.355 - 1.112)
Mar. '94 - Apr. '94	2.773 (2.258 - 3.433)	0.437 (0.238 - 0.716)
Apr. '94 - May '94	3.129 (2.498 - 3.953)	0.559 (0.300 - 0.942)
May '94 - June '94	3.010 (2.530 - 3.627)	0.214 (0.133 - 0.331)
June '94 - July '94	0.758 (0.635 - 0.919)	0.112 (0.071 - 0.175)
July '94 - Aug. '94	0.389 (0.308 - 0.495)	0.061 (0.038 - 0.094)
Aug. '94 - Sept.'94	3.995 (3.390 - 4.727)	0.973 (0.629 - 1.425)
Total	55.026 (46.373 - 65.951)	11.392 (6.803 - 17.765)

Period	Somatic biomass (g)	Somatic production
Sept.'93 - Oct. '93	6.182 (5.732 - 6.671)	1.432 (1.052 - 1.869)
Oct. '93 - Nov. '93	5.532 (5.158 - 5.937)	1.137 (0.842 - 1.472)
Nov. '93 - Dec. '93	4.180 (3.812 - 4.591)	0.442 (0.321 - 0.580)
Dec. '93 - Feb. '94	5.668 (4.809 - 6.692)	1.975 (1.183 - 3.005)
Feb. '94 - Mar. '94	3.910 (3.304 - 4.639)	0.373 (0.221 - 0.568)
Mar. '94 - Apr. '94	1.677 (1.440 - 1.956)	0.247 (0.149 - 0.370)
Apr. '94 - May '94	1.878 (1.593 - 2.217)	0.313 (0.188 - 0.478)
May '94 - June '94	1.997 (1.798 - 2.219)	0.133 (0.097 - 0.175)
June '94 - July '94	0.503 (0.451 - 0.561)	0.068 (0.051 - 0.094)
July '94 - Aug. '94	0.275 (0.226 - 0.337)	0.043 (0.030 - 0.065)
Aug. '94 - Sept.'94	2.788 (2.436 - 3.196)	0.700 (0.494 - 0.950)
Total	34.592 (30.758 - 39.016)	6.863 (4.628 - 9.626)

Period	Gonad biomass (g)	Gonad production
Sept.'93 - Oct. '93	0.699 (0.333 - 1.148)	0.335 (0.016 - 0.778)
Oct. '93 - Nov. '93	0.741 (0.419 - 1.128)	0.291 (0.032 - 0.638)
Nov. '93 - Dec. '93	0.746 (0.402 - 1.192)	0.133 (0.023 - 0.292)
Dec. '93 - Feb. '94	1.011 (0.706 - 1.417)	0.470 (0.180 - 0.900)
Feb. '94 - Mar. '94	0.701 (0.485 - 0.992)	0.089 (0.036 - 0.169)
Mar. '94 - Apr. '94	0.290 (0.207 - 0.399)	0.057 (0.022 - 0.110)
Apr. '94 - May '94	0.338 (0.236 - 0.472)	0.076 (0.029 - 0.148)
May '94 - June '94	0.651 (0.522 - 0.805)	0.024 (-0.001 - 0.048)
June '94 - July '94	0.165 (0.132 - 0.206)	0.013 (0.001 - 0.024)
July '94 - Aug. '94	0.075 (0.049 - 0.112)	0.016 (0.003 - 0.027)
Aug. '94 - Sept.'94	0.772 (0.540 - 0.955)	0.198 (0.093 - 0.342)
Total	6.140 (4.031 - 8.825)	1.702 (0.434 - 3.476)

Period	Gamete biomass (g)	Gamete production
Sept.'93 - Oct. '93	2.800 (2.511 - 3.161)	0.538 (0.425 - 0.707)
Oct. '93 - Nov. '93	2.432 (2.158 - 2.783)	0.410 (0.324 - 0.554)
Nov. '93 - Dec. '93	1.719 (1.501 - 2.015)	0.145 (0.112 - 0.203)
Dec. '93 - Feb. '94	2.749 (2.029 - 3.790)	1.065 (0.529 - 1.972)
Feb. '94 - Mar. '94	1.901 (1.395 - 2.641)	0.201 (0.098 - 0.375)
Mar. '94 - Apr. '94	0.805 (0.611 - 1.078)	0.133 (0.067 - 0.236)
Apr. '94 - May '94	0.913 (0.669 - 1.264)	0.170 (0.083 - 0.316)
May '94 - June '94	0.362 (0.210 - 0.603)	0.057 (0.037 - 0.108)
June '94 - July '94	0.090 (0.052 - 0.152)	0.031 (0.019 - 0.057)
July '94 - Aug. '94	0.039 (0.033 - 0.047)	0.002 (0.005 - 0.002)
Aug. '94 - Sept.'94	0.484 (0.414 - 0.576)	0.058 (0.042 - 0.133)
Total	14.295 (11.583 - 18.110)	2.810 (1.741 - 4.663)

Table 10. Calorics production of *C. radiata* at Anjuna (cal/m^2)

Period	No. of Days	Mean Density (/m^2)
Sept.'93 - Oct. '93	28	11.55
Oct. '93 - Nov. '93	28	10.40
Nov. '93 - Dec. '93	19	7.90
Dec. '93 - Feb. '94	83	9.85
Feb. '94 - Mar. '94	23	8.35
Mar. '94 - Apr. '94	32	5.25
Apr. '94 - May '94	41	5.05
May '94 - June '94	17	4.80
June '94 - July '94	35	2.50
July '94 - Aug. '94	30	1.70
Aug. '94 - Sept.'94	29	7.55
Total	365	

Period	Total biomass (cal)	Total production
Sept.'93 - Oct. '93	47977 (42478 - 54425)	11552 (7466 - 16788)
Oct. '93 - Nov. '93	43224 (38285 - 48894)	9229 (5995 - 13344)
Nov. '93 - Dec. '93	33117 (28462 - 38856)	3631 (2305 - 5399)
Dec. '93 - Feb. '94	46882 (37749 - 58769)	17210 (9380 - 28511)
Feb. '94 - Mar. '94	32374 (25937 - 40832)	3246 (1766 - 5392)
Mar. '94 - Apr. '94	13809 (11313 - 16987)	2138 (1183 - 3481)
Apr. '94 - May '94	15554 (12498 - 19517)	2746 (1485 - 4580)
May '94 - June '94	14875 (12377 - 18061)	1061 (641 - 1660)
June '94 - July '94	3746 (3104 - 4576)	560 (339 - 875)
July '94 - Aug. '94	1977 (1561 - 2525)	322 (201 - 496)
Aug. '94 - Sept.'94	20053 (16979 - 23768)	5002 (3258 - 7308)
Total	273589 (230843 - 327210)	56697 (34018 - 87832)

Period	Somatic biomass (cal)	Somatic production
Sept.'93 - Oct. '93	30545 (28224 - 33082)	7181 (5206 - 9462)
Oct. '93 - Nov. '93	27402 (25462 - 29504)	5712 (4173 - 7465)
Nov. '93 - Dec. '93	20808 (18890 - 22959)	2227 (1604 - 2956)
Dec. '93 - Feb. '94	28083 (23960 - 32971)	9494 (5719 - 14354)
Feb. '94 - Mar. '94	19365 (16456 - 22837)	1790 (1076 - 2713)
Mar. '94 - Apr. '94	8335 (7193 - 9670)	1189 (722 - 1782)
Apr. '94 - May '94	9300 (7931 - 10918)	1508 (904 - 2287)
May '94 - June '94	9810 (8683 - 11086)	645 (445 - 888)
June '94 - July '94	2472 (2179 - 2807)	342 (235 - 473)
July '94 - Aug. '94	1410 (1148 - 1742)	238 (160 - 342)
Aug. '94 - Sept.'94	14031 (12188 - 16179)	3630 (2563 - 4956)
Total	171563 (152312 - 193755)	33957 (22811 - 47677)

Period	Gonad biomass (cal)	Gonad production
Sept.'93 - Oct. '93	3450 (1607 - 5736)	1638 (32 - 3892)
Oct. '93 - Nov. '93	3653 (2025 - 5626)	1427 (119 - 3203)
Nov. '93 - Dec. '93	3676 (1932 - 5963)	660 (89 - 1482)
Dec. '93 - Feb. '94	4989 (3463 - 7008)	2244 (818 - 4379)
Feb. '94 - Mar. '94	3458 (2378 - 4902)	423 (154 - 830)
Mar. '94 - Apr. '94	1438 (1021 - 1978)	275 (101 - 529)
Apr. '94 - May '94	1665 (1157 - 2332)	361 (131 - 706)
May '94 - June '94	3217 (2603 - 3956)	114 (18 - 245)
June '94 - July '94	816 (656 - 1010)	63 (11 - 135)
July '94 - Aug. '94	381 (241 - 588)	68 (27 - 134)
Aug. '94 - Sept.'94	3661 (2675 - 4932)	1008 (443 - 1816)
Total	30403 (19757 - 44032)	8282 (1943 - 17351)

Period	Gamete biomass (cal)	Gamete production
Sept.'93 - Oct. '93	13982 (12647 - 15607)	2733 (2228 - 3435)
Oct. '93 - Nov. '93	12169 (10898 - 13764)	2090 (1703 - 2676)
Nov. '93 - Dec. '93	8633 (7640 - 9934)	743 (612 - 961)
Dec. '93 - Feb. '94	13809 (10326 - 18790)	5471 (2843 - 9778)
Feb. '94 - Mar. '94	9551 (7103 - 13092)	1032 (536 - 1850)
Mar. '94 - Apr. '94	4036 (3099 - 5339)	674 (359 - 1170)
Apr. '94 - May '94	4589 (3410 - 6267)	877 (449 - 1587)
May '94 - June '94	1848 (1091 - 3019)	302 (177 - 526)
June '94 - July '94	458 (269 - 759)	154 (92 - 267)
July '94 - Aug. '94	185 (173 - 195)	16 (14 - 20)
Aug. '94 - Sept.'94	2361 (2117 - 2657)	364 (251 - 535)
Total	71623 (58773 - 89422)	14458 (9263 - 22804)

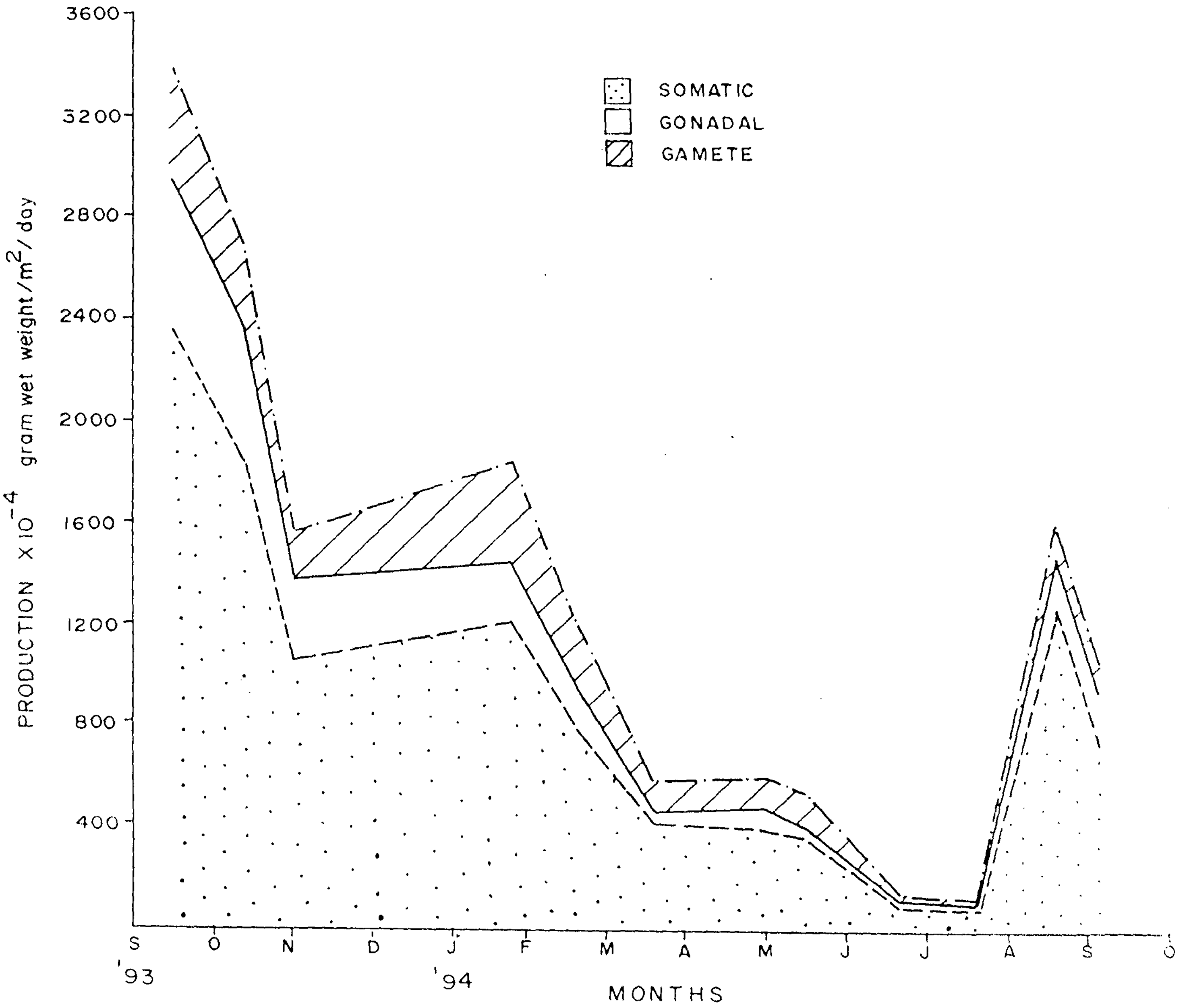


Fig. 46. The estimated monthly production values (in g wet weight / m^2 / day) for the limpet population from September'93 to October '94.

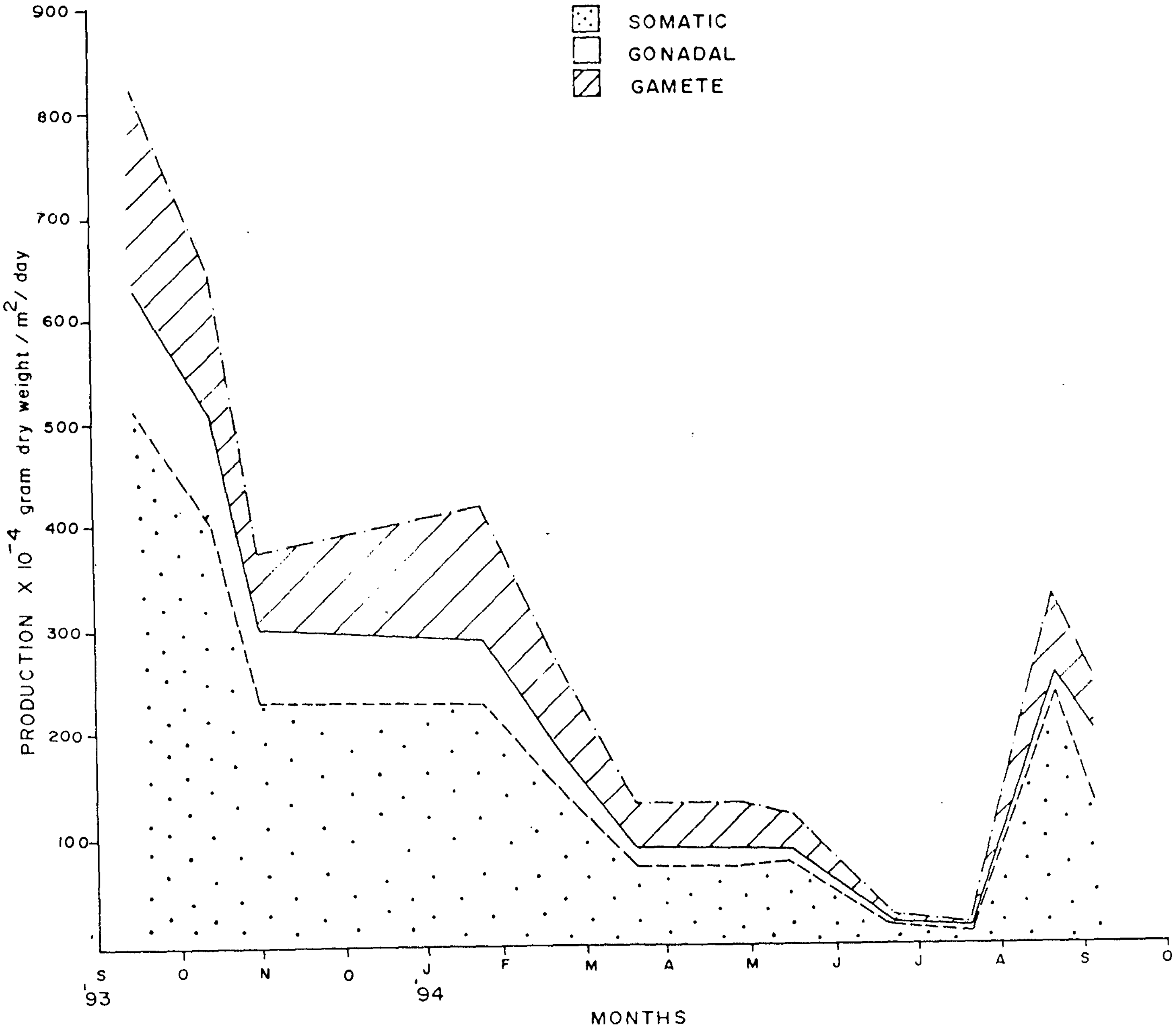


Fig. 47. The estimated monthly production values (in g dry weight / m² / day) for the limpet population from September '93 to October '94.

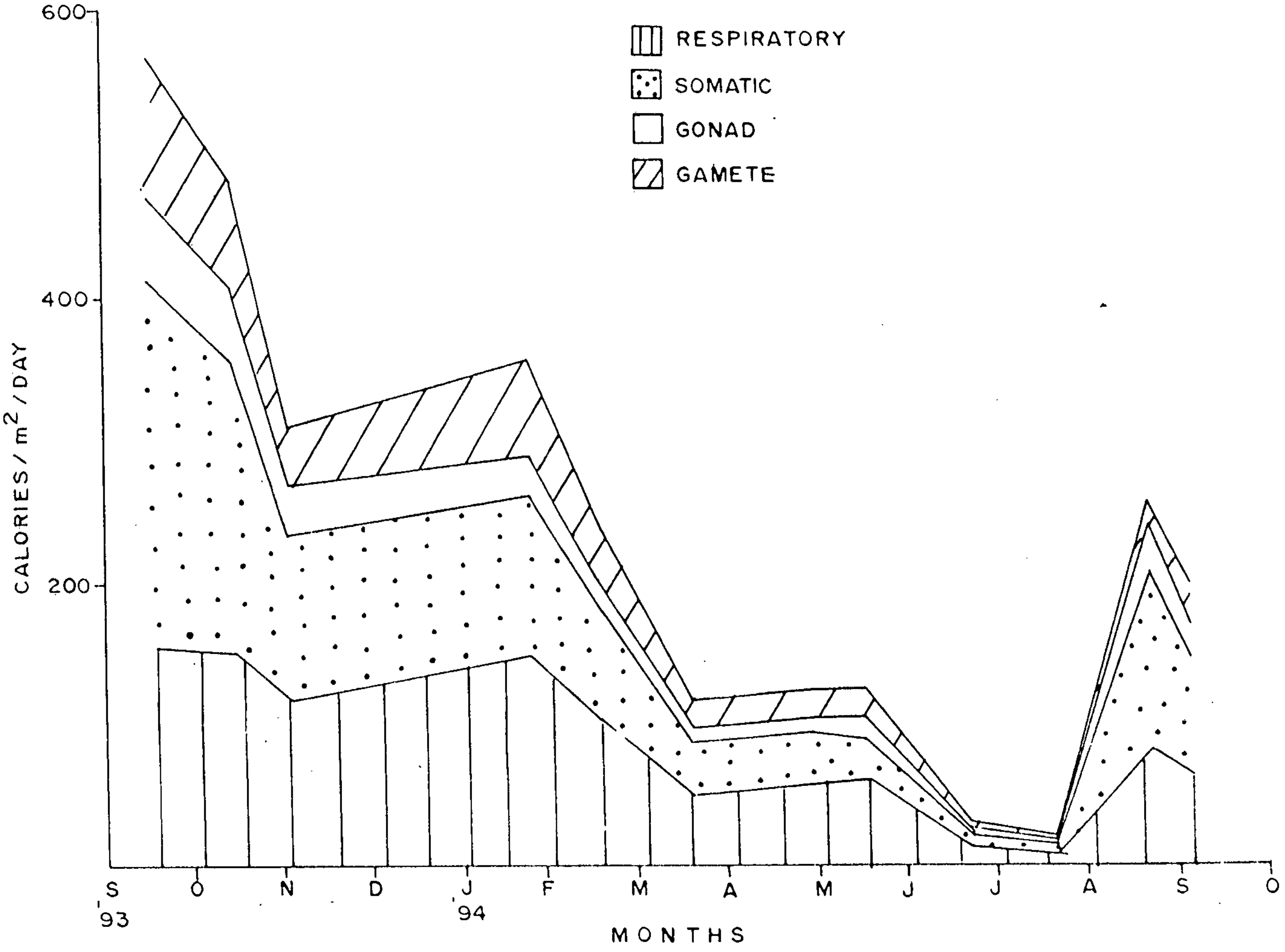


Fig. 48. The estimated monthly production and respiration values (in calories / m² / day) for the limpet population from September '93 to October '94.

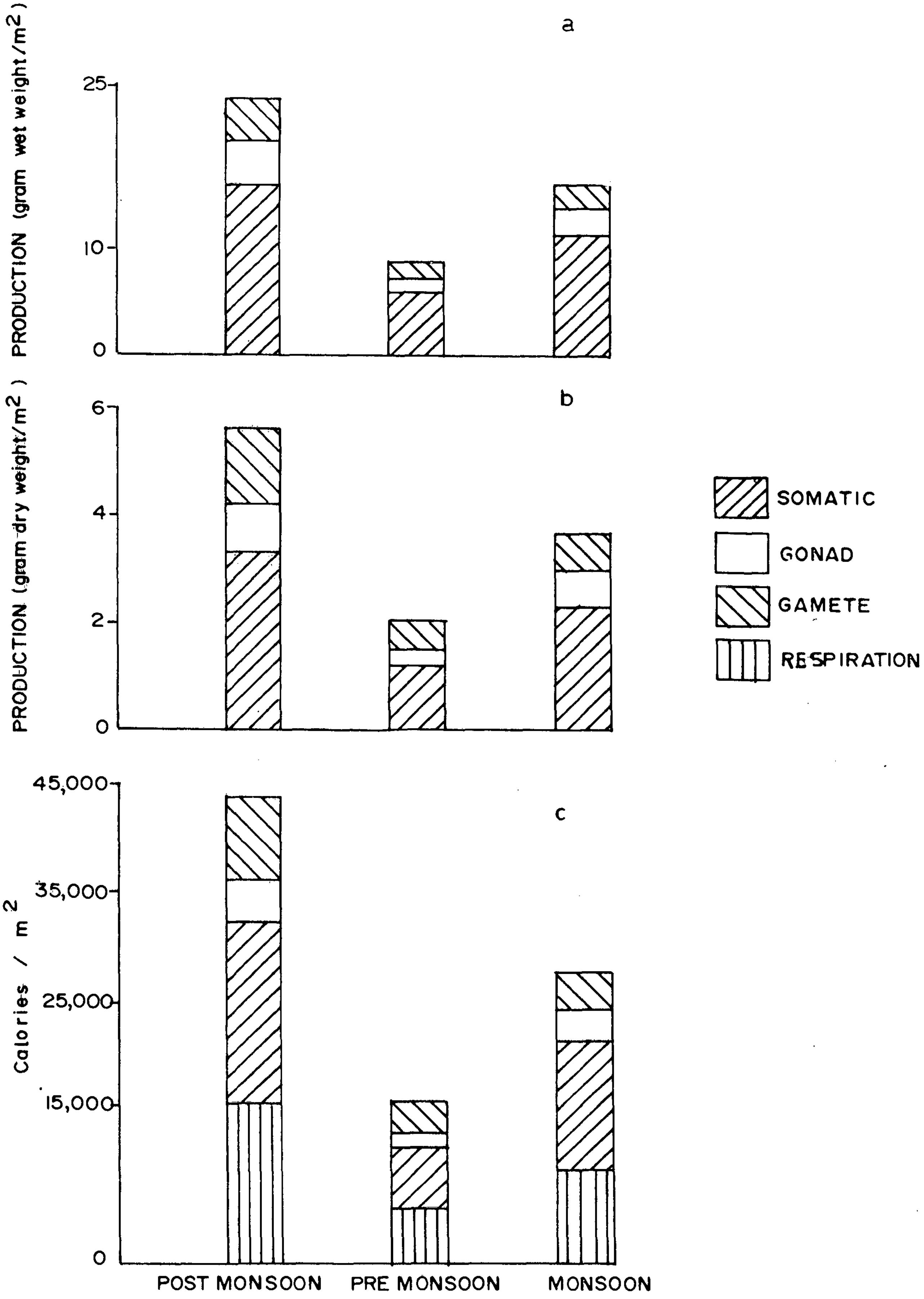


Fig. 49. The estimated seasonal production and respiration values for the limpet population from September '93 to October '94 in (a) g wet weight/m^2 (b) g dry weight/m^2 (c) calories /m^2.

respectively.

5.1.2 SOMATIC PRODUCTION

Maximum monthly somatic production was recorded in September-October '93 with values of 7.083 g wet wt/m², 1.534 g dry wt/m² and 7694 cal/m². Lowest values were recorded in July-August '94 with values of 0.253 g wet wt/m², 0.043 g dry wt/m² and 238 cal/m² (Fig. 46 to Fig. 48). Somatic production was highest during the post-monsoon season and lowest during the peak monsoon season (Fig. 48).

5.1.3 GONADAL PRODUCTION

The energy channelled into reproduction results in the growth of the gonads and the liberation of spawned gametes. The most satisfactory method of estimating the energy released as spawned gametes would be to collect the gametes as they are liberated and estimate their biomass and energy content. As this is impractical, indirect methods have to be adopted. In the present study, maximal gonadal values, assumed to represent limpets that had not yet liberated gametes, were used to estimate the biomass of gonads before spawning. This method has its drawbacks as is evidenced by the negative value obtained for the confidence limit of gonad dry weight during May-June '94 (Table 9). Nevertheless, in the absence of other methods, these values can be considered as realistic estimates.

Monthly gonad production in terms of wet weight, dry weight and calories were highest in September-October '93 with values being 1.767 g/m², 0.359 g/m² and 1755 cal/m² respectively. Lowest values were recorded in June-August '94 with values of 0.031 g/m², 0.011 g/m² and 54 cal/m² respectively (Fig. 46 to Fig. 48). Gonad production was highest during the post-monsoon season and lowest during the peak monsoon season (Fig. 48).

Maximum gamete production was recorded in September-October '93 with values of 1.350 g wet wt/m², 0.576 g dry wt/m² and 2928 cal/m² and lowest values were recorded in July-August '94 with values of 0.025 g wet wt/m², 0.002 g dry wt/m² and 16 cal/m² (Fig. 46 to Fig. 48). Gamete production was highest during the post-monsoon season and lowest during the peak monsoon season (Fig. 48).

5.1.4 RESPIRATION

The respiration budget of *C. radiata* presented are based on laboratory experiments and hence may not represent the actual respiration of the field population at Anjuna. However, this has been the standard practice for estimating energy lost through metabolism. Figure 50 and Fig. 51a illustrates the respiratory rates of different sizes of *C. radiata* collected from Anjuna at three temperatures *viz.* 23°C, 28°C and 35°C. The slopes of the

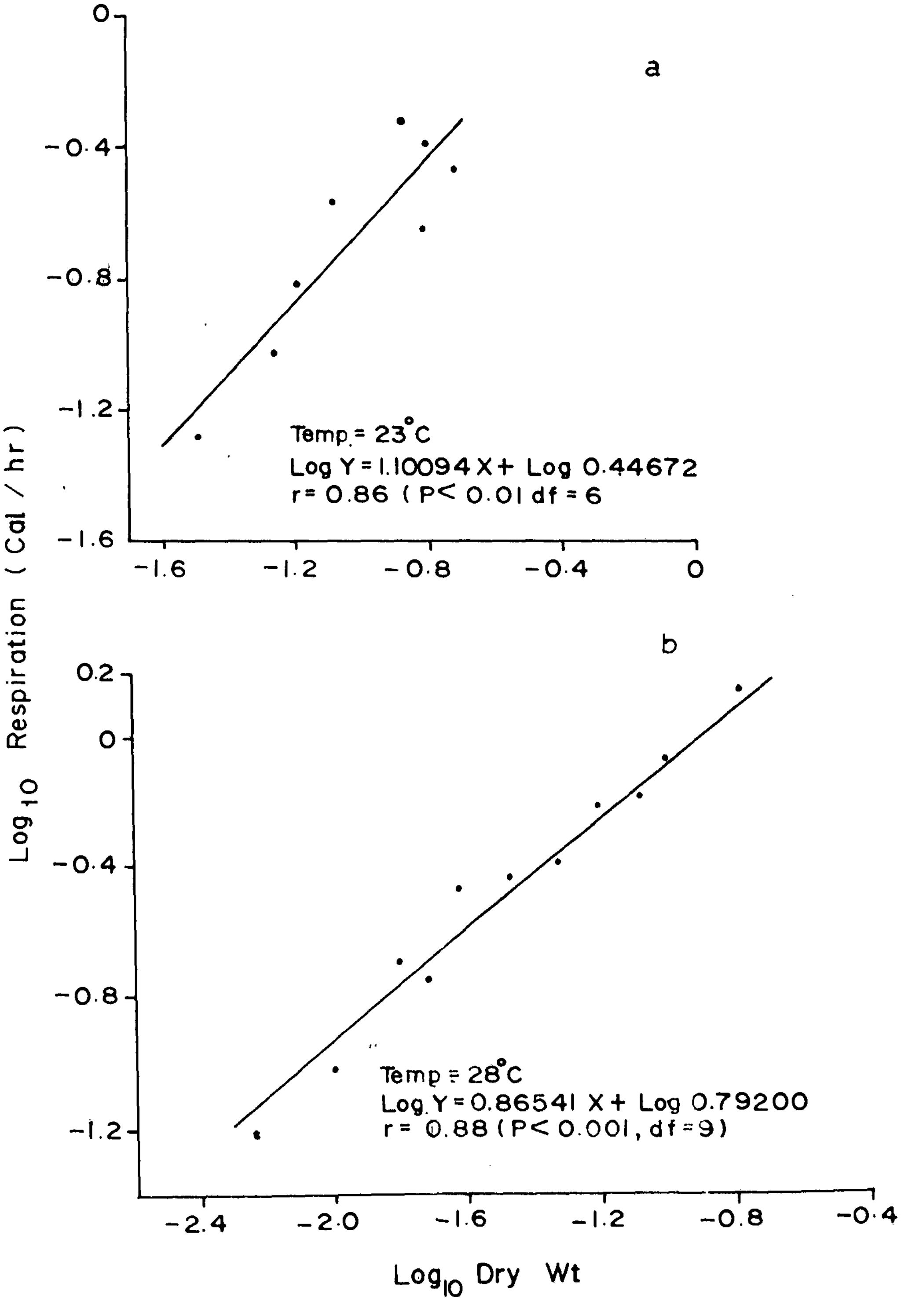


Fig. 50. The relationship between dry tissue weight and respiratory rate in calories at (a) 23°C (b) 28°C .

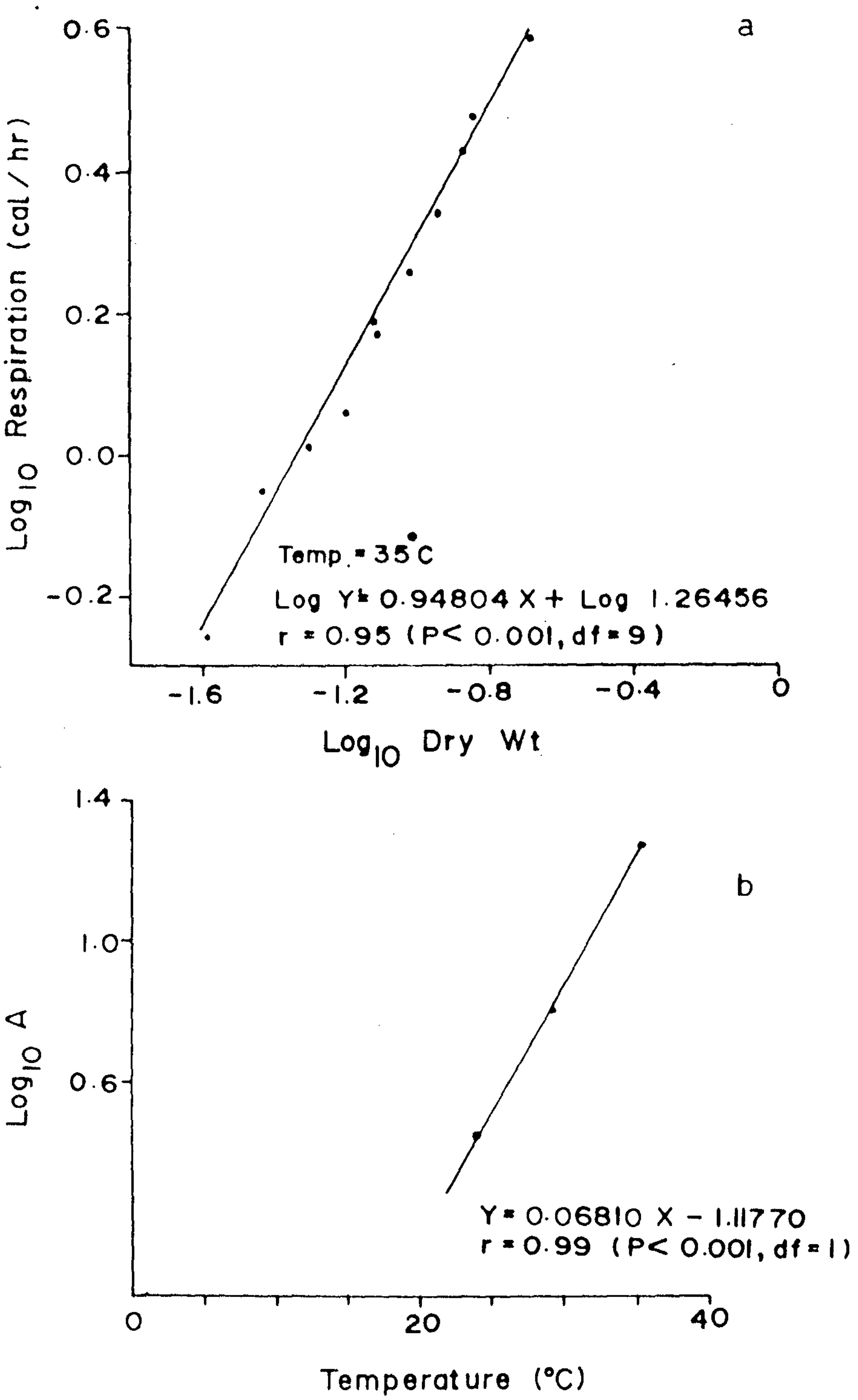


Fig. 51a. The relationship between dry tissue weight and respiratory rate in calories at 35°C.

b. The relationship between log A and temperature.

regression lines of the respiratory rate (Y) *versus* tissue dry weight (X) equations at the different temperatures are indicated in the plots. The respiratory rates increased with increasing temperature and increasing limpet biomass.

The respiratory rate at 23°C ranged from 0.01082 ml O_2/hr to 0.09903 ml O_2/hr. The shell length of the limpets ranged from 16mm to 30mm. The dry weight of the limpet 0.032 g to 0.192 g. It was difficult to obtain the respiratory rate of limpets below a shell length 16mm since the respiration values were very low. The respiratory rate at 28°C ranged from 0.01242 ml O_2/hr to 0.23471 ml O_2/hr. The shell length of the limpets varied from 10mm to 30mm while their dry weight varied from 0.006g to 0.163g. The respiratory rate at 35°C ranged from 0.09673 ml O_2/hr to 0.84887 ml O_2/hr. The shell length of the limpets ranged from 10mm to 30mm. Their dry weights ranged from 0.018g to 0.179g. Respiration rates of limpets at temperatures below 23°C and above 35°C could not be measured as they could not be acclimatized to these extreme temperatures, even though temperature changes were brought about gradually.

The relationship between $\log_{10}A$ and temperature was linear (Fig. 51b) and the regression equation was used to estimate A at different temperatures recorded in the study area during the study period.

Based on the above detailed laboratory experiments, the estimated respiratory losses for the limpets at Anjuna is given in Table 11 along with their 95% confidence limits. The respiratory losses in cal/m²/day of the population are graphically depicted in Fig. 48. Respiration losses were highest during the post-monsoon season and lowest during the monsoon season (Table 11).

5.2 ENERGY BUDGET AND CONVERSION EFFICIENCIES

The summary of the energy budget components are presented in Table 12. The monthly growth values are standardised (30 days) to enable comparisons. As no data is available for January '94, data of December '93 to February '94 was averaged to obtained the monthly estimates. The trends indicated above can also be seen. It can be seen that most of the gametes are released during the post-monsoon season. Assimilation values are high at the end of the monsoon season and during the post-monsoon season and low during the monsoon season.

Conversion efficiencies are also presented in the same Table. The respiration efficiency (R/A) was low during the monsoon and early part of the post-monsoon season. The net growth efficiency (P/A) was slightly high, particularly during the end of the monsoon and the begining of the post-monsoon seasons. The reproductive efficiency (P*rep*/P) was high during part of the pre-monsoon and post-monsoon season and generally low during the monsoon season. Reproductive effort (P*rep*/A) was low during part of the monsoon season.

Table 11. Respiration budget of *C. radiata* at Anjuna

Period	Days	Hours	Density (/m²)	Mean Temp (°C)	Respiration losses (calories)
Sept.'93 - Oct. '93	28	672	11.55	29.55	4305 (3836 - 4839)
Oct. '93 - Nov. '93	28	672	10.40	30.55	4223 (3792 - 4707)
Nov. '93 - Dec. '93	19	456	7.90	30.50	2233 (1938 - 2581)
Dec. '93 - Feb. '94	83	1992	9.85	29.60	12269 (10314 - 14625)
Feb. '94 - Mar. '94	23	552	8.35	29.75	2424 (2028 - 2904)
Mar. '94 - Apr. '94	32	768	5.25	30.35	1555 (1324 - 1831)
Apr. '94 - May '94	41	984	5.05	31.15	2335 (1963 - 2782)
May '94 - June '94	17	408	4.80	29.85	1028 (912 - 1160)
June '94 - July '94	35	840	2.50	28.10	496 (438 - 562)
July '94 - Aug. '94	30	720	1.70	28.50	237 (191 - 296)
Aug. '94 - Sept.'94	29	696	7.55	28.80	2387 (2055 - 2779)
Total	365	8760			33492 (28790 - 39066)

Table 12. Summary of the energy budget (cal/m²) of *C. radiata* at Anjuna

Period	Somatic Pg	Gonad *Pr*	Gamete *Prg*	*Prep* (*Pr*+*Prg*)	Total P=*Prep*+Pg
Sept.'93 - Oct. '93	7694	1755	2928	4683	12377
Oct. '93 - Nov. '93	6120	1529	2239	3768	9888
Nov. '93 - Dec. '93	3516	1042	1175	2217	5733
*Dec. '93 - Jan. '94	3432	811	1977	2788	6220
*Jan. '94 - Feb. '94	3432	811	1977	2788	6220
Feb. '94 - Mar. '94	2335	552	1346	1898	4233
Mar. '94 - Apr. '94	1115	258	632	890	2004
Apr. '94 - May '94	1103	264	642	906	2009
May '94 - June '94	1138	201	533	734	1872
June '94 - July '94	293	54	132	186	479
July '94 - Aug. '94	238	68	16	84	322
Aug. '94 - Sept.'94	3756	1043	377	1420	5175
Sept.'93 - Sept.'94	33957	8282	14458	22740	56697

			Efficiency			
Period	Respiration R	Assimilation A = P+R	R/A	P/A	*Prep*/P	*Prep*/A
Sept.'93 - Oct. '93	4613	16990	0.274	0.728	0.378	0.276
Oct. '93 - Nov. '93	4525	14413	0.314	0.686	0.381	0.261
Nov. '93 - Dec. '93	3526	9259	0.381	0.619	0.387	0.239
*Dec. '93 - Jan. '94	4435	10655	0.416	0.584	0.448	0.262
*Jan. '94 - Feb. '94	4435	10655	0.416	0.584	0.448	0.262
Feb. '94 - Mar. '94	3162	7395	0.427	0.572	0.448	0.257
Mar. '94 - Apr. '94	1458	3462	0.421	0.579	0.444	0.257
Apr. '94 - May '94	1709	3718	0.460	0.540	0.451	0.244
May '94 - June '94	1814	3686	0.492	0.508	0.392	0.199
June '94 - July '94	425	904	0.470	0.530	0.388	0.206
July '94 - Aug. '94	237	559	0.424	0.576	0.261	0.150
Aug. '94 - Sept.'94	2238	7413	0.302	0.698	0.274	0.192
Sept.'93 - Sept.'94	33492	90189	0.371	0.629	0.401	0.252

* from Dec. '93 - Feb. '94 data

5.3 DISCUSSION

There are only a few published reports on the energy budgets of intertidal molluscan species. This is mainly because of the practical difficulties. not only in the field but also in the laboratory. in estimating the various components in order to produce an annual budget for a population. Among the most complete studies are those of Hughes (1970) on the bivalve. *Scrobicularia plana* on the North Wales coast and Wright & Hartnoll (1981) on the limpet. *Patella vulgata* on the rocky shores in the Isle of Man. Survey of the literature reveals that there are practically no reports on the complete energy budget of rocky shore intertidal benthic species along the Indian coast. The results obtained in the present study are thus compared with those obtained elsewhere by other investigators.

In many cases. as in the present study. consumption (C) has been difficult to estimate due to practical considerations and has to be indirectly estimated. This problem particularly applies to limpets. which are herbivorous. feeding on microflora (Branch. 1981). Further. faecal production (F) in limpets has also seldom been estimated and hence the absorption efficiency cannot be accurately assessed. Branch (1981) reports approximate absorption efficiencies ranging from 72% to 93% in the case of *Patella* spp.. Another component of the energy budget that has not been measured in the present study is that of urine and other exudates (U). The excretory products of limpets are ammonia. urea and uric acid and though its contribution to the energy flow is unknown, it is likely to be a very small fraction of the total budget (Branch, 1981).

5.3.1 PRODUCTION

The present study reveals that the various production estimates of the *C. radiata* population at Anjuna vary not only from season to season but also monthly. These variations can be attributed to variations of environmental factors such as temperature, wave action, availability of food and the population structure. Production will occur only if the food supply exceeds the metabolic demands of the animal and is likely to be affected by temperature and the quality and abundance of food (Hughes, 1986).

The population structure, which takes into account not merely densities but mainly the population age group distribution which in turn reflects the physiological condition of the individual, influences production rates. For example, Ansell (1982), reported an increase in the absorption efficiency of *Polinices alderi* as it enters the reproductive stage. In the present study, *C. radiata* exhibited asymptotic growth at a shell length of approximately 34 mm. As the limpet ages, reproductive effort reaches its maximum, somatic production declines and the animal attains its asymptotic size (Branch, 1981).

Highest production values were recorded during the post-monsoon season. During this season, temperatures are moderate, wave action is also moderate and food (algal growth) is maximum. As a result, the limpets not only invested the energy consumed for somatic growth but also for reproductive growth which includes gonadal development and gamete production.

Though temperatures are lower during the monsoon season, wave action is intense and food is scarce. The scarcity of food is mainly due to the intense wave action which can easily dislodge not only macroalgal species but also any diatom or microalgal species from the rock surface. The limpets, during this season, would therefore be expending more energy searching for food. The low respiration losses during this season is due to the change in the population structure which could have arisen either due to mortality or migration out of the study area. It is difficult to ascertain which of the two was largely responsible.

During the pre-monsoon season, though food is available, *albeit* to a lesser extent than during the post-monsoon season, and wave action moderate, temperatures are higher. An increase in temperature will in turn increase the metabolic activity, urging the individuals to forage for more food. Paradoxically, estimates on respiration losses suggests that energy required for metabolic activities during the post-monsoon season are much higher than that required during the pre-monsoon.

5.3.2 P/B RATIO

The calculation of P/B ratios allows populations of different biomass to be compared. The rationale of calculating P/B ratios was to obtain common patterns. For example, Robertson (1979) related annual P/B values with life span. It was also hoped that production could be calculated merely from biomass as the estimation of production is cumbersome. An attempt in this regard was made by Banse and Mosher (1980). Unfortunately, there are many factors that influence this ratio. Low temperatures, slow growth rates and varying predation rates lower the ratio (*e.g.* see Workman, 1983). Variations in growth rates and predation alter the ratio by causing changes in the age distribution. Population growth rate and size structure are the major factors influencing P/B ratios. P/B ratios are often related to energy requirements of a given species. However, much of the energy actually consumed by an organism goes not to increase its biomass but for respiration. Moreover, a significant proportion of energy can be utilized for gamete production as in *Patella peroni* (Parry, 1982).

In the present study, the annual P/B ratio of *C. radiata* at Anjuna was 0.207. The annual P/B ratio of limpets at other localities are given in Table 13. It can be seen that the value appears to be low compared to other limpets. Further, it is not correlated with life span as suggested by Zaika (1972) and Wright and Hartnoll (1981) in their analysis of molluscan species.

TABLE 13

A comparison of the annual P/B ratios of different species of limpets in other localities.

Species	P	B	P/B	Source
Cellana radiata	237	114	0.207	Present study
Patella vulgata				
1974	153	339	0.45	Wright & Hartnoll, 1981
1975	175	353	0.49	
1976	164	346	0.47	
Patella vulgata				
(1978) site 1	97	106	0.90	Workman, 1983
(1979) site 1	152	90	1.70	
(1978) site 2	7.5	101	0.1	
(1979) site 2	64	90	0.7	
Nacella delesserti	2003	1804	1.11	Blankley & Branch, 1985.
Nacella concinna	2.9*	13.7*	0.2	Picken, 1980.

* Values in g/m²

Investigators studying the macrofauna of the Indian coast have been assuming that a generalized estimate of benthic production could be obtained by doubling the standing crop (biomass) as suggested by Sanders (1956). However, Ansell *et al.* (1977), studying the macrobenthos of sandy beaches along the southwest coast of India, obtained P/B ratios of 5.88 and 10.29 for two species of bivalves (*Donax* spp.). The present study suggests that for limpets in the study area, production is about five times the standing crop.

5.3.3 RESPIRATION

The respiration rate of *C. radiata* in the laboratory obtained in the present study are low. Rao (1980) obtained values ranging from 0.112 ml O_2/hr to 0.423 ml O_2/hr at 25°C for limpets 15mm to 28mm in length and wet weight of 0.161 g to 0.963 g. In the present study, the limpets appeared to be inactive and repetition of the laboratory experiments yielded the same results.

Oxygen consumption rate (R) is related to body weight by the equation $R = A \cdot w^b$, where 'b' has a generalized value of 0.75 (Hemmingsen, 1960). The value of 'b' (0.97) obtained for *C. radiata* is higher than those obtained for other limpets. In the case of limpets at Waltair, Rao (1980) obtained a 'b' value of 0.68. It it thus most likely that the respiration rates have been underestimated.

Further, it must be noted that in calculating the respiration losses of the energy budget of the field population of *C. radiata*, it is assumed that the oxygen consumed by limpets is the same during ebb and flow tide. Diurnal variations in oxygen consumption (Newell, 1979; Rao, 1980) has not been taken into account while drawing up the budget. Nevertheless, the trends obtained should remain valid.

The respiratory losses expressed in terms cal/m²/day show a decreasing trend from the post-monsoon season to the monsoon season. The metabolic rates in relation to seasons has already been discussed earlier.

Englemann (1966) reported that in poikilotherms there is a correlation between metabolism (R) and production (P) which could be described by the following regression equation:

$$\log_{10} R = 0.62 + 0.86 \log_{10} P$$

Values obtained in this paper appears to fit the line quite well (Fig. 52). Englemann's regression equation thus adequately relates metabolism to production and though the equation has been modified by MacNeil and Lawton (1970), it can be refined only after more data on different species accumulate.

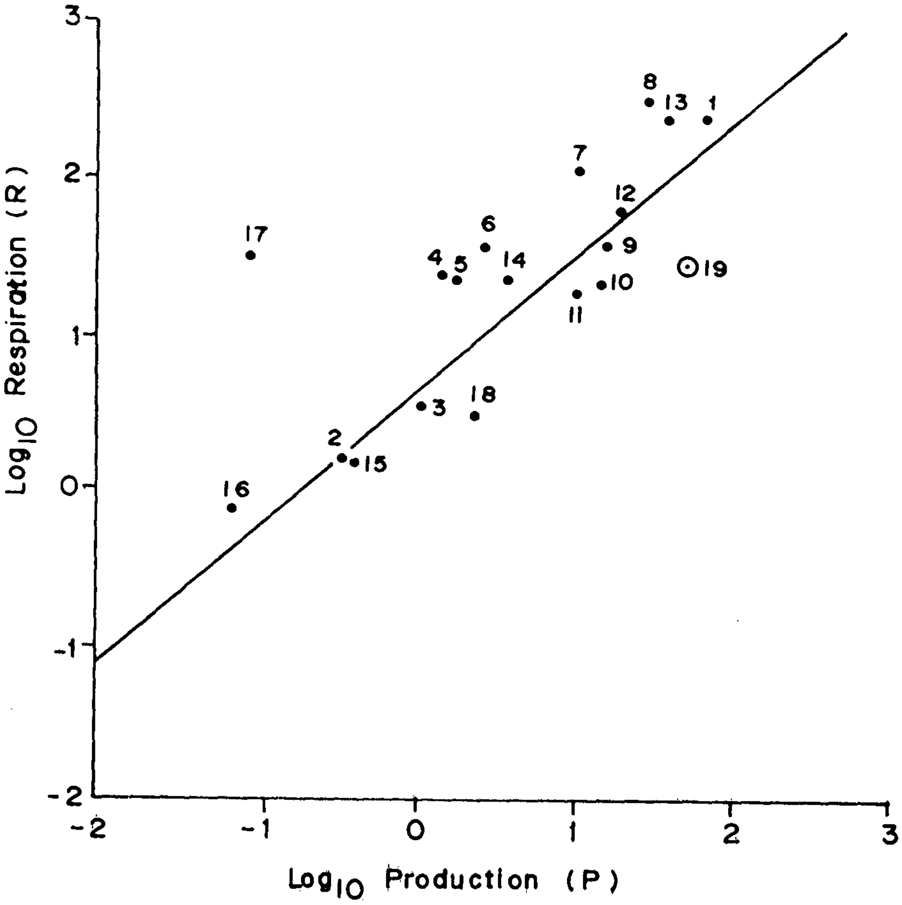


Fig. 52. The relationship between production and respiration for different species. (After Hughes, 1970).

1. *Scrobicularia plana* (Hughes, 1970)
2. *Myrmica rubra* (Stradling, 1968)
3. *Lasius niger* (Stradling, 1968)
4. *Leuciscus leuciscus* (Mann, 1965)
5. *Perca fluviatilis* (Mann, 1965)
6. *Gobio gobio* (Mann, 1965)
7. *Rutilus rutilus* (Mann, 1965)
8. *Alburnus alburnus* (Mann, 1965)
9. *Modiolus dimissus* (Kuenzler, 1961)
10. *Philaenus spumarius* (Weigert, 1964)
11. *Orchelimum fidicinium* (Smalley, 1960)
12. Nematodes (Teal, 1962)
13. *Littorina irrorata* (Odum & Smalley, 1959)
14. Orthoptera (Odum et al., 1962)
15. Oribatei (Engelmann, 1961)
16. *Philaenus spumarius* (Weigert, 1964)
17. *Pogonomyrmex badius* (Golley & Gentry, 1964)
18. *Onychiurus procampatus* (Healey, 1967)
19. *Cellana radiata* (Present study)

5.3.4 ENERGY BUDGET

Results obtained on the various components of the energy budget helps in understanding the energy flow in the population of the limpet, *C. radiata*, at Anjuna. It must however be borne in mind that energy budgets are not fixed and vary on account of the influence of several abiotic and biotic factors whose roles are still being studied. From energy budgets quantitative data on the energy partitioning for different biological processes can be obtained.

The energy budget can be used to estimate energy allocated for reproduction. Most limpets investigated so far by other workers have a well defined short breeding season as seen in invertebrates that are broadcast fertilizers (Giese, 1959). In such cases accurate estimate of energy partitioning for gamete production can be obtained. On the other hand, it is difficult to obtain estimates in the case of limpets that breed continuously or are reproductively active over a larger period of the year such as *C. radiata* (Rao, 1973), *Patelloida alticostata* and *P. latistrigata* (Creese, 1980). Hughes (1971a) indirectly estimated the amount of gonad spawned by *Fissurella barbadensis* by assuming that the limpets emptied their gonads twice a year. In the present study another indirect method was followed to quantify the amount of gonad spawned on the assumption that the maximum gonad values recorded represented individuals that have not yet spawned.

It is thus clear from the present study that *C. radiata* is a continuous breeder with peak spawning during the post-monsoon season. Along the East coast of India, the peak spawning period for *C. radiata* is in December and February (Rao, 1975a). Data obtained in the present study revealed that the limpet releases about 60% of its gametes during October-February and the remaining are liberated during the other two seasons, *viz.* pre-monsoon and post-monsoon, in roughly equal proportions (about 20%). Peak spawning during post-monsoon and early part of pre-monsoon would enable the larvae to settle down before the harsh conditions that prevails with the onset of monsoons. It would also ensure a constant food supply. Quinn (1988b), found the reproductive cycles and reproductive output in *Siphonaria diemenensis* to be strongly correlated with seasonal differences in the availability of food, a relationship confirmed by experimental manipulations. The peak spawning during the post-monsoon season incurs high expenditure of energy. It is noteworthy that Patil & Mane (1982) in their studies on *Cellana rota* at Ratnagiri, situated on the west coast of India, have reported spawning from November-April which was preceded by an increase in biochemical reserves during May-September.

The energy budget of other limpets and their various efficiencies are presented in Table 14 for comparison. It can be seen that the production values of limpets fluctuate widely. The high somatic production values obtained in this study are comparable with those of Hughes (1971). It can also be seen that R is too low. Crisp (1984) pointed out that all laboratory

Table 14. Components of energy budgets for limpets (kcal/m²/yr)

Species	Location	Pg	Pr	Prg	Prep	P
Cellana radiata	Anjuna, Goa, India	34.0	8.3	14.5	22.7	56.7
Cellana tramoserica	San Remo, Australia					
(1971-72)		3.5	0.5	8.8	9.3	12.9
(1972-73)		2.9	0.7	7.5	8.2	11.1
Notaçmea petterdi	San Remo, Australia	4.3	0?	12.4	12.4	16.7
Patelloida alticostata	San Remo, Australia	0.7	0.1	1.1	1.2	1.9
Patella peroni	San Remo, Australia	21.7	5.2	61.9	67.1	88.8
Patella vulgata	Isle of Man, U.K.	16.3	?	22.7	22.7	39.0
Patella vulgata	Robin Hood Bay, U.K.					
(1978) site 1		17.8	5.4	?	5.4	23.2
(1979) site 1		27.7	8.6	?	8.6	36.3
(1978) site 2		-3.0	4.8	?	4.8	1.8
(1979) site 2		12.2	3.1	?	3.1	15.3
Fissurella barbadensis	Barbados, West Indies	46.0	5.3	?	5.3	51.3

Species	R	A	Efficiency				Source
			R/A	P/A	*Prep/P*	*Prep/A*	
Cellana radiata	33.5	90.2	0.37	0.63	0.40	0.25	Present study
Cellana tramoserica							Parry, 1982
(1971-72)	59.5	72.4	0.82	0.18	0.72	0.13	
(1972-73)	61.4	72.4	0.85	0.15	0.74	0.11	
Notacmea petterdi	95.0	107.4	0.88	0.16	0.74	0.11	Parry, 1982
Patelloida alticostata	10.0	11.9	0.84	0.16	0.64	0.10	Parry, 1982
Patella peroni	163.1	259.9	0.65	0.35	0.76	0.27	Parry, 1982
Patella vulgata	119.0	158.0	0.75	0.25	0.58	0.14	Wright & Hartnoll, 1981
Patella vulgata							Workman, 1983
(1978) site 1	-	-	-	-	0.23	-	
(1979) site 1	-	-	-	-	0.24	-	
(1978) site 2	-	-	-	-	2.67	-	
(1979) site 2	-	-	-	-	0.20	-	
Fissurella barbadensis	139.3	190.6	0.73	0.27	0.10	0.03	Hughes, 1971a

methods of measuring respiration suffer from the defect that the animals are constrained in an unnatural situation and thus may not represent their respiration in the field. Some investigators have had to double the respiration rate to balance the energy budget (Carefoot, 1967; Wright & Hartnoll, 1981). In the present study, as C was not measured, no internal checks on the accuracy of the various estimates could be made. Due to the underestimation of R, other estimates such as assimilation (A) and efficiency ratio using these R estimates cannot be considered accurate. Nevertheless, the monthly as well as seasonal trends holds good. Reproductive effort of *C. radiata* was observed to be low when compared to most other limpets as it is a continuous breeder.

In the present study, consumption (C) could not be estimated and hence has to be indirectly estimated by summing up the remaining components of the energy budget. Results obtained indicate that the *C. radiata* population at Anjuna would have a mean annual consumption requirement of at least 90 kcal. Considering the error in the R values, energy requirements would be still more. Dhargalkar *et al.* (1980) report a mean caloric content of 4971 cal/g for Chlorophyceae of the Maharashtra coast. The mean consumption requirements of the *C. radiata* population at Anjuna would therefore be at least 18 g dry wt/year.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The present study dwells on some ecological aspects of the of the limpet *Cellana radiata* (Born. 1778) on the rocky shores of Anjuna (Goa) from September 1993 to May 1995. During this period studies were carried out on its eco-biology, population structure and energy budget.

The substratum at Anjuna comprises of metagrewacke and laterite rocks. The study area, which projects seawards upto around 60m remains exposed during an average low tide. The limpets are thus subjected to variations in temperature and desiccation. Temperatures are highest during the pre-monsoon season followed by the post-monsoon and monsoon seasons. Salinity values were high during pre-monsoon and low during monsoon. Dissolved oxygen values registered a low during monsoon and high during post-monsoon.

The distribution of *C. radiata* suggests that it is mainly a midtidal inhabitant. Its upper limit seems to be determined by physical factors while its lower limit is probably determined by competition. Shell characteristics *viz.* shell length, shell width, shell height, distance from apex to anterior end and distance from apex to posterior end were significantly correlated. Using regression analysis, shell length was related with somatic and total biomass. These equations were used to nondestructively estimate the biomass, along with the 95% confidence limits, of the limpet population at Anjuna. The difference between total biomass and gonadal biomass was an estimate of gonadal biomass.

C. radiata is a generalist herbivore as deduced from gut content analyses. The chief source of food were diatoms, macroalgae like *Enteromorpha* spp. and *Chaetomorpha* sp.. Laboratory observations suggested that feeding and locomotion were interlinked.

Field observations revealed that *C. radiata* is active only during the flood tide, regardless of time of the day. There is virtually no movement during low tide. Activity begins with the first splashes of the high tide. The mean daily displacement rates recorded in February and May were 25.3 ± 8.15 cm/day and 40.5 ± 11.10 cm/day respectively. Limpets never retraced their paths on succeeding excursions and re-oriented their positions at the end of each excursion. This enables them to avoid areas previously grazed. It was also observed that *C. radiata* is a temporary homer. Homing was observed during May (pre-monsoon season) and considered as an adaptation against desiccation.

The population structure of *C. radiata* at Anjuna was analysed by statistically fitting component Gaussian curves to the size frequency distribution. Shifts in modal peaks revealed the presence of four population groups during the study period from September '93 to October '94. The first group was observed from September '93 to February '94 with their mean shell length increasing from 21.52mm to 28.32mm. The second group could be traced upto July '94 with their mean size increasing from 17.31mm to 29.50mm. The third group seen from March '94 to October '94 had their mean size increased from 20.07mm to 24.95mm. The last group was registered in September '94 and grew from 17.78mm to 20.08mm. Smaller individuals were recorded during the month of September, December and March.

Results obtained on the fate of individually marked limpets along the Indian coast are reported for the first time. Marked limpets disappeared from the study area and reappeared after gaps of 41-200 days, thereby suggesting that the limpets migrated out of the study area. Some marked limpets were found amidst boulders adjacent to the study area. Shell growth of *C. radiata* followed the von Bertlanffy growth model. The von Bertlanffy growth parameters *viz.* L_∞, the asymptotic shell length and the annual growth coefficient, K, was 39.41mm and 0.089 respectively. The maximum shell length recorded at the study site was 36.75mm which is close to the estimated L_∞ value. The growth curve in *C. radiata* is asymptotic with the smaller limpets growing faster than the larger ones. The limpet attains a shell length of 25mm, 34.72mm, 37.79mm, 38.85mm and 39.41mm during the first, second, third, fourth and fifth year respectively. The sharp decline in the growth rate after the first year could probably be attributed to the increased allocation of energy for reproduction. The theoretical life span of the limpet, *i.e.* when it attains its asymptotic shell length, was estimated to be five years. Limpets beyond a shell length of 34mm were very rarely observed in the field thereby suggesting that survival beyond the second year is remote. The causes of mortality could not be ascertained.

Growth rates in *C. radiata* was estimated by two methods: by analysing shifts in modal peaks and by tagging of limpets in the field. Shifts in modal peaks indicated that growth rates values were 1.32 mm/month for pre-monsoon, 1.22 mm/month for monsoon and 1.60 mm/month for post-monsoon. Growth rates measured by tagging individual limpets in the field produced similar results. Using data obtained from tagged limpets, the growth coefficient, K, during these respective seasons were 0.09, 0.07 and 0.11 respectively. The growth rate were comparable with that reported for *C. radiata* inhabiting the Waltair coast. Growth rates varied seasonally. Variability in the seasonal growth rate is attributed to the availabilty of food and the temperature regime. Algal growth at Anjuna is seasonal with growth beginning at the post-monsoon period and reaching a peak during February - March. The decrease in growth rate during the pre-monsoon season despite abundance of food could possibly be explained by the increase in the severity of temperatures during this period.

The components of the energy budget estimated *viz.* production and respiration reveal varying monthly and seasonal values which could be attributed to factors like temperature, wave action, availability of food and the population structure. As the limpet ages reproductive effort reaches its maximun and somatic production declines and the animal approaches its asymptotic size. *C. radiata* exhibited such an asymptotic growth at a shell length of approximately 34mm.

Production values were highest during the post-monsoon with the environmental conditions being congenial for them with moderate wave action and abundant food. Lowest values were recorded during peak monsoon when the food is scarce and wave action is intense. Annual total, somatic, gonadal and gamete production from September 1993 to September 1994 were 56697 cal/m², 33957 cal/m², 8282 cal/m² and 14458 cal/m² respectively. The 95% confidence limits of these estimates are also presented. Production values are also expressed in terms of wet weight and dry weight to enable comparison with published literature. Consumption estimates, indirectly computed, suggested a mean annual consumption requirement of at least 90 kcal equivalent to 18g dry weight of algae for the field population of limpets at Anjuna.

The respiratory rates of limpets in the laboratory increased with increasing temperature and increasing limpet biomass. The respiratory rate at 23°C, 28°C and 35°C ranged from 0.01082 ml O_2/hr to 0.09903 ml O_2/hr, 0.01242 ml O_2/hr to 0.23471 ml O_2/hr and 0.09673 ml O_2/hr to 0.84887 ml O_2/hr respectively. The b exponent value of the relation between respiration (R) and weight (w) *viz.* $R = aw^b$ was higher than that reported for *C. radiata* on the Waltair coast. Estimates of respiratory losses, based on laboratory observations and applied to the field population of *C.*

radiata during the study period, suggested that they did not reflect actual metabolic energy losses. Their trends were however considered valid. Estimated annual respiratory losses from September 1993 to September 1994 was 33492 cal/m². Production and respiration were correlated and fitted Englemann's regression equation adequately. The estimated P/B ratio (0.207) was, however, lower when compared to other species and was not related to life span as suggested by some authors. Annual production in limpets was thus roughly equivalent to five times its mean annual standing stock.

Respiration efficiency was low during the monsoon and early part of the post-monsoon season. The net growth efficiency was slightly high, particularly during the end of the monsoon and the begining of the the post-monsoon seasons. Reproductive efficiency was high during part of the pre-monsoon and generally low during the monsoon season. Reproductive effort was low during part of the monsoon season.

Sexes, in *C. radiata*, are separate with no secondary sexual characters. They can be distinguished by the colour of the gonads, with males having creamish yellow gonads and females having greenish ovaries. Differences between shell characteristics of sexes were statistically insignificant. The sizes of males and females overlapped and the sex ratio was 1:1. The limpet attains sexual maturity at a shell length between 10-15mm (3 to 5 months old). It is a continuous breeder as indicated by the gonadal index, analysis of population structure and gamete production. The gonadal index suggested that the limpet spawns throughout the year with a peak during the post-monsoon and ebb during peak monsoon, enabling the larvae to settle during a favourable period when food is abundant.

Energy apportioned for reproduction indicated that *C. radiata* released 60% of gametes being released during the post-monsoon season. The remaining is spawned over during the other two seasons in roughly equal proportions. Peak spawning during post-monsoon season would ensure a continuation in the progeny. The reproductive effort was found to be lower than that reported for other species and was attributed to its continuous breeding activity.

Spawning of *C. radiata* was observed in the laboratory during December. The main stimulus for spawning appeared to be the change in ambient temperature. There was no pairing of sexes as observed in some other limpet species. Gametes were shed through the anterior end; males spawning first, followed by females. Sperms were released as a jet and eggs as a brown patch. Fertilised eggs metamorphosed but all the stages could not be observed. Only three survived, one of them attaining a shell length of 4.6mm after 40 days.

In brief, *C. radiata* in the present study conformed to traits exhibited by other tropical species. It had a faster growth rate, attained early sexual maturity and was a continuous breeder.

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