ENERGETICS OF THE CHITON *SYPHAROCHITON PELLISERPENTIS* FROM A SHELTERED SHORE AT KAIKOURA

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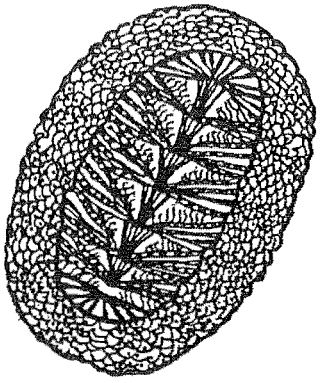
CHITONS

THESE MOLLUSCS OR LIVing fossils have plates like old armour on the outside and a ridge of muscle which keeps them clinging to the rocks on or below low-water mark. The foot on the underside is edible, though not substantial, and must be cleaned almost immediately it has been removed. It does not keep well once prised away from its habitat, so scrape and wash the foot thoroughly, and think about dinner within the next couple of hours at most!

Small chitons are eaten raw by many Island peoples and they may also be ground and included in soups and chowders. Alternatively, pound the flesh with a hammer to tenderise, dip in a mixture of egg and crushed cereal or breadcrumbs and fry quickly. ●



Snakeskin chiton
(Sypharochiton pelliserpentis)

From:

"SIMPLY LIVING, a gatherers' guide to New Zealand's fields, forests and shores", by Gwen Skinner.

A.H. & A.W. Reed, Wellington. 1981.

CONTENTS

ABSTRACT

Energy budgets are reported for high- and low-shore groups of the chiton *Sypharochiton pelliserpentis* from a sheltered shore, Kaikoura Peninsula. All components of the budget were measured; i.e., growth production (P_g), mucous production (P_m), reproductive production (P_r), respiration (R), defaecation (F), excretion (U) and consumption (C_m). Previous molluscan energetics studies have usually ignored P_m and U, and calculated consumption by summing all other terms. The largest single component of the budgets of both groups was mucous production which accounted for about 72% of assimilated energy, whereas respiration (generally assumed to be the largest component of energy expenditure by animals) accounted for only about 23% of assimilation. This finding shows the importance of mucous production in molluscan energetics. Assimilation efficiencies of both chiton groups (89 and 93%) are higher than those reported generally for other molluscs. Differences between the budgets occurred in faecal production and reproductive effort. High-shore chitons defaecated only 7% of their ingested energy, compared with 11% egestion by low-shore chitons. High-shore chitons expended 4.2% of their assimilated energy (excluding P_m) on reproduction, whereas low-shore chitons expended only 2.6%. High-shore chitons exhibited some adaptations enabling them to maintain consumption in the face of reduced available feeding time, and reduce metabolic costs in the face of exposure to higher environmental temperatures. Annual energy flow through the high-shore group (509 kJ m^{-2}) was only about a third of the low-shore flow (1375 kJ m^{-2}). Measured consumption (C_m) on the high shore was 8% lower than the estimate of consumption obtained by summing all other components (C_s), whereas on the low shore, C_m was 9.6% higher. The small differences between C_m and C_s for both groups suggest that the reported budgets are accurate representations of energy flow through the groups. The inclusion of mucous production in the budgets for *S. pelliserpentis* is the main cause of differences between these budgets and budgets reported for other herbivorous gastropods.

1. INTRODUCTION

Understanding the energy flow within an ecosystem is basic to an appreciation of the functioning of the system itself. The primary tool for such studies is the energy budget and the basic equation for the components of an energy budget, according to IBP terminology, (Petrusewicz and Macfadyen, 1970), is as follows:

$$C = P_g + P_r + R + F + U,$$

where C is the energy content of the food consumed; P_g is the energy content of somatic tissue added to the population by growth, recruitment and migration; P_r is the energy content of the gametes liberated during spawning; R is the energy lost as a result of respiration; F is the energy content of the faeces; and U is energy lost as urine, dissolved organic matter and other exudates. Recent studies, however, have shown that the energy content of mucous secretion, P_m, is another important component of molluscan energetics (Branch, 1981; Edwards and Welsh, 1982). Previously, this component had been either ignored, or estimated and included in the U term. Since mucus is produced from assimilated ingested material, this component is more properly placed within production and this is how it is treated here. Also in this study, I follow Kofoed (1975b) and assume that assimilation (A) equals P + R + U. Most previous studies of energy budgets have either ignored U or estimated it and combined it with the F component. However, unlike faeces, excreta are derived from assimilated material and should, therefore, be included with the other components of A.

Ideally, <u>all</u> components of the budget should be measured, rather than some being determined by shortfall differences. All components have been measured here, enabling consumption to be measured both directly (C_m) and indirectly by summing all other components (C_s); thus providing a valuable internal check on the accuracy of the overall budget.

The energetics of the major gastropod grazers of various marine and fresh water communities have been studied (e.g., Paine, 1971; Hunter, 1975; Kamler and Mandecki, 1978; Wright and Hartnoll, 1981). However, chitons have received

little attention in this regard mainly because they are major grazers in only a few ecosystems, e.g., the black leather chiton, *Katharina tunicata*, is a major grazer on parts of the west coast of North America (Himmelman and Carefoot, 1975; Paine, 1980). In New Zealand, however, the chiton fauna is numerous and diverse (Powell, 1979), and one species, *Sypharochiton pelliserpentis* (Quoy and Gaimard, 1835), is common throughout the country (Morton and Miller, 1968). In a previous study, I have shown that high- and low-shore *S. pelliserpentis* groups possess different population characteristics and different adaptations to environment (Horn, 1981, 1982). Populations of *Sypharochiton* exhibit different age-structures and size-frequency distributions (Boyle, 1970; Horn, 1981); hence, energy budget differences may be anticipated. Previous studies of gastropods have shown that species living at different shore heights (Paine, 1971) or in neighbouring localities (Hughes, 1971b) can exhibit intraspecific differences in energy budget characteristics. I decided to see whether the same trends were present in chitons by investigating separately during the 1982 calendar year the energy budgets of high- and low-shore groups of *S. pelliserpentis* in Mudstone Bay, Kaikoura.

This study reports for the first time on the energy budget of a chiton. The work is novel further in that all components of the energy budget are measured. In addition, the data measured enable an intraspecific examination of the effects of shore level on energy expenditure, a topic which has received little attention previously.

2. METHODS

2-1 Study Area

The study area was Mudstone Bay, in South Bay, Kaikoura Peninsula (173° 41' 10" E; 42° 25' 30" S), a shore sheltered from wave action and consisting of glauconitic siltstone (Fig. 1) (Rasmussen, 1965). *Sypharochiton pelliserpentis* occurs throughout the intertidal at Mudstone Bay and two groups, one designated as "low-shore" and the other as "high-shore" were selected for study. Low-shore chitons were distributed between Low Water Neap and Extreme Low Water Spring in a boulder-strewn channel which was about 9m long and 3m wide (Fig.2). Associated biota were mainly molluscs, crustaceans, annelids and dense stands of macro-algae (particularly *Hormosira banksii*). High-shore chitons were between Mean Sea Level and High Water Neap and occupied small crevices and depressions in gently sloping platforms (Fig. 3). Macroalgae were rare and associated fauna included limpets (*Cellana denticulata*), trochids (*Melagraphia aethiops*), anemones (*Actinia tenebrosa*), and barnacles (*Chamaesipho columna* and *C. brunnea*).

2-2 Population Structure

At monthly intervals for 12 months, the body lengths of 300 individuals selected at random from each chiton group were measured using hand-held calipers. The data were sorted into 1mm size-classes and used to construct length-frequency histograms. To offset errors in measurements introduced as a result of animal flexibility on rough substratum, the length-frequency histograms were smoothed using a moving average of three, (i.e., the number in size-class x was plotted as the mean of the raw data numbers in size-classes x-1, x, and x+1).

Chiton age was estimated using growth-check lines deposited in the shell-valves. These were visible externally and also on polished cross-sections of the shell-valves, and were assumed to be laid down annually (Horn, 1981). This method was used to age the chitons *Lepidochitona cinereus* (Baxter and Jones, 1978) and *Sypharochiton pelliserpentis* (Horn, 1981). The lengths and

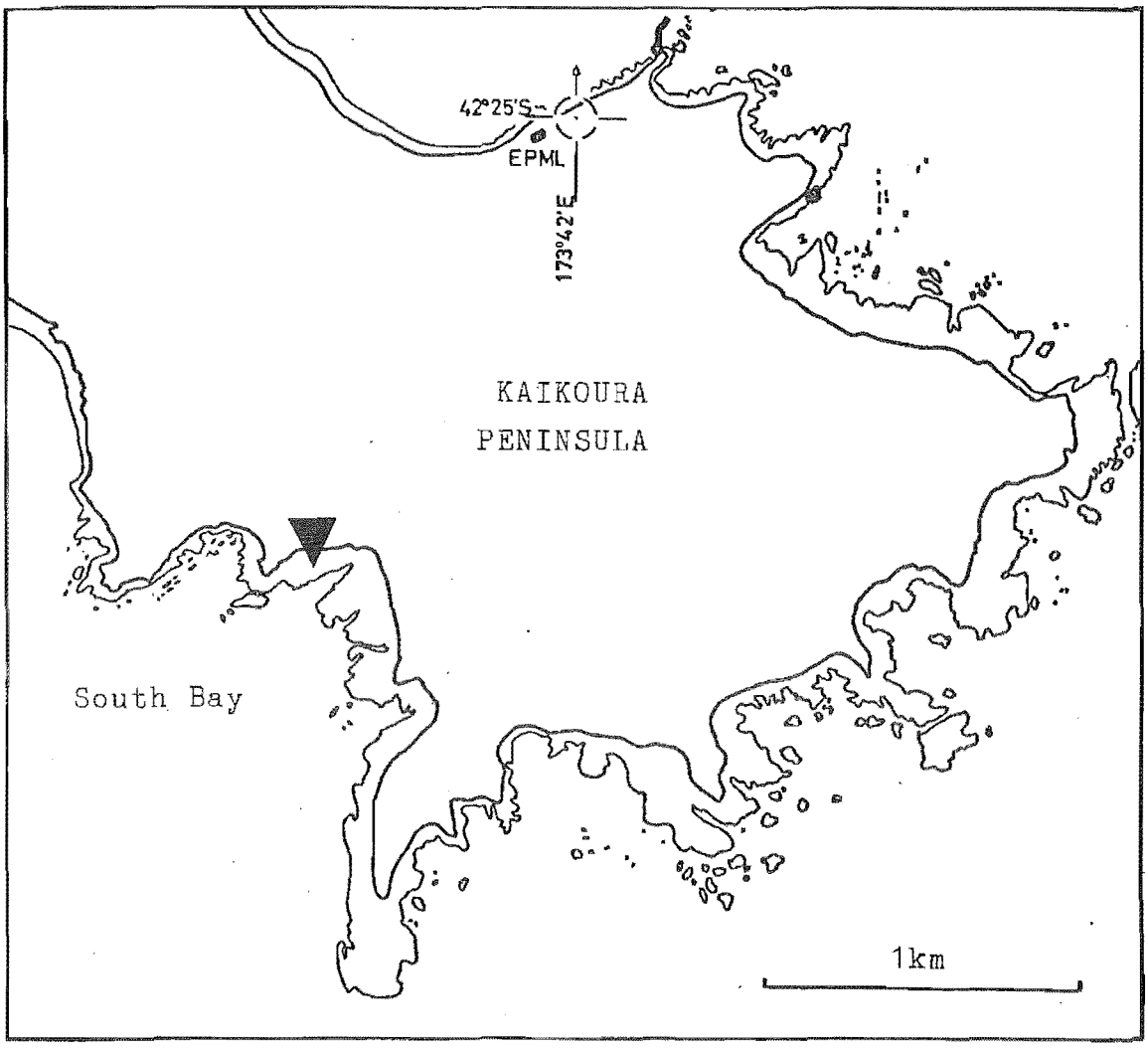
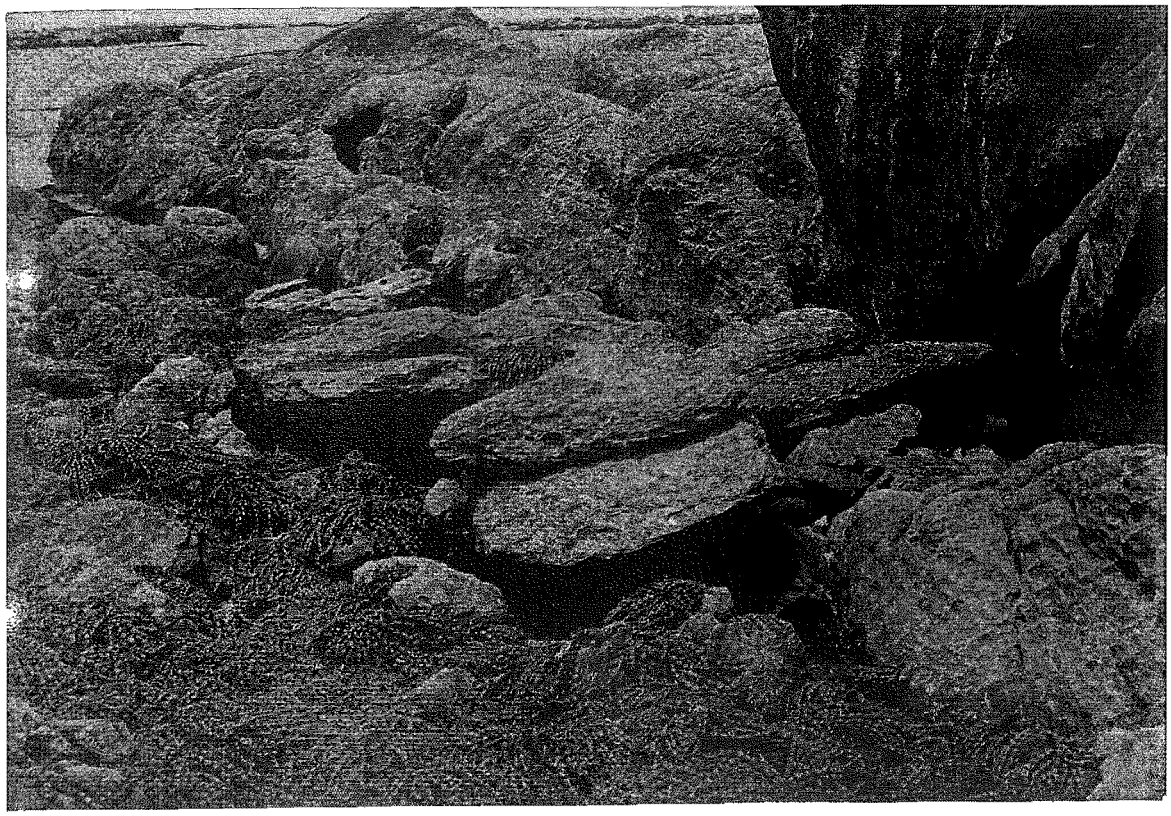
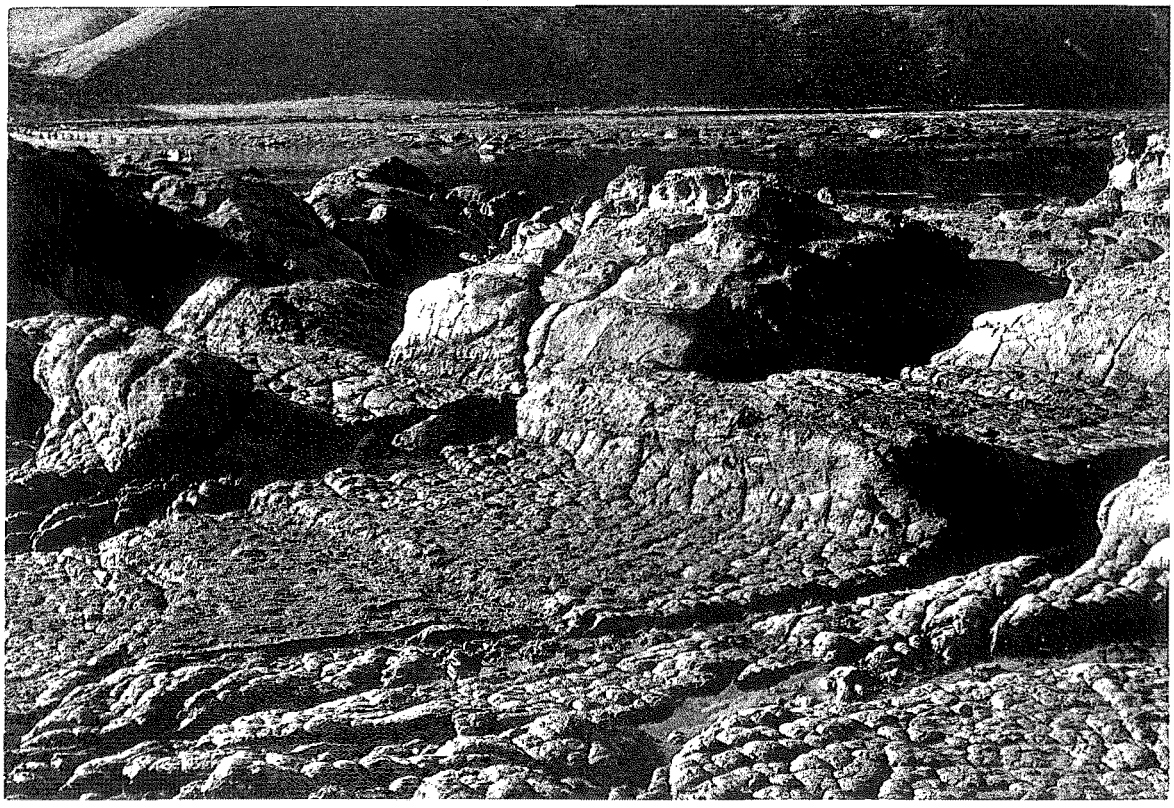


Fig. 1 - Kaikoura Peninsula, showing the position of the sheltered shore study site (arrowed) in Mudstone Bay, South Bay. EPML - Edward Percival Marine Laboratory.

Fig. 2 - The low-shore site, Mudstone Bay, Kaikoura, showing one side of the channel containing loose boulders with dense stands of the alga *Hormosira banksii*, during a low spring tide in August 1982.

Fig. 3 - The high-shore site, Mudstone Bay, Kaikoura, showing the gently sloping, creviced platforms and higher bedrock pinnacles, in August 1982.





inferred ages of 132 chitons from each group were determined in December 1981. Mean lengths of each year-class were calculated and fitted, using Ford-Walford plots (Crisp, 1971), to the Bertalanffy growth equation,

$$\ell_t = L_\infty - (L_\infty - L_o)\, e^{-Kt},$$

where ℓ_t is the estimated body length at age t, L_∞ and L_o are constants representing the theoretical maximum length and length at zero age, respectively, and K is a constant related to the rate of approach to length L_∞. This model was chosen because it best describes growth of animals having a short pre-reproductive period relative to longevity (Brody, 1945; Ricker, 1958; Yamaguchi, 1975; Tanaka and Kikuchi, 1980)

To check the reliability of the calculated growth equations, six high-shore chitons that exhibited homing behaviour were monitored on the shore. Their actual growth increments over one year were compared with the expected increments as calculated from the growth equation. It was not possible to monitor the growth of low-shore chitons in the field as they did not home and were highly mobile; marking and recovery of specimens was not practical over a one year period. Consequently, five low-shore animals were kept in a tidal aquarium (modified from Ottaway, 1975) and their annual growth increments were measured and compared with the predicted values.

2-3 Activity Patterns

Accurate estimation of an energy budget requires knowledge of activity patterns. To estimate these for chitons, activities were categorised using the simple criteria of "moving" or "not moving", and "feeding" or "not feeding".

The two chiton groups were observed during January, April, July and October 1982, during daylight and darkness, and when the animals were immersed, emersed on wet rock, and on dry rock. There were thus six time-state categories. For each category, at least 20 animals were observed for a minute (i.e., 20 minutes of observations) and the proportions of time spent moving and/or feeding were noted. Feeding was detected using a microphonic sensor (Boyden and Zeldis, 1979) held for one minute on the rock surface less than 50mm from

each chiton. Vibrations caused by friction of the chiton's toothed radula on the rock surface within 100mm of the sensor were amplified and could be heard clearly using headphones. Night observation were made with a dim red torch.

2-4 Energy Budget

2-4-1 General

Chitons from the study areas already described were used to obtain data on population structure, mortality, feeding rates and activity. For other aspects of the study, chitons were taken from shores in Mudstone Bay experiencing similar physical conditions to the specified study areas, but not immediately adjacent to them. This prevented any unnatural disturbance of population structure.

In the following laboratory experiments, dry weights of somatic tissue and gonad were determined after drying at 75°C to constant weight. Percentage ash content of tissue was determined after heating in a muffle furnace at 500°C for 4h. All weights were accurate to ±0.1mg. Calorific content of animal and plant matter was determined using a Parr No. 1411 combustion calorimeter. Material containing more than 70% ash was mixed with an approximately equal weight of benzoic acid to ensure complete combustion, and a correction for endothermy was applied (Paine, 1966). The joule and kilojoule are used here to express results since they are the SI units for energy. Many previous studies, however, have worked in calories, so in Table 17 the energy budgets for *Sypharochiton* are presented in kJ and kcal to allow comparison with those for other species. (One kcal = 4.186 kJ.)

Meteorological data (air temperature and sunshine hours) were obtained from the Kaikoura meteorological station, which is about 1.2km from Mudstone Bay and 100m above sea level.

Individual components of the energy budgets for high- and low-shore chitons were obtained using the following methods.

2-4-2 Consumption (C)

Rates of consumption for grazing molluscs have proved difficult to measure, due mainly to the problems with quantifying the intake of microflora. Southward (1964) measured consumption by calculating the weight of laboratory-cultured algal film that was grazed by limpets, but concluded that for reasons unknown, the laboratory conditions changed the normal feeding behaviour of the animal. Wright and Hartnoll (1981) attempted to measure consumption in the field by calculating the weight of microalgae grazed from slates bolted on the shore within cages. However, they concluded that ingestion of algae on natural rock was less than on the more profusely covered slates, and suggested that transfer of the limpets to the slates could affect feeding behaviour. With these considerations in mind, I attempted to estimate consumption by measuring the area of substratum cleared by each radular rasp, the radular rasping rate, and the energy available per unit area of substratum.

To measure area cleared per rasp, microalgae were cultured on perspex plates by holding them for about a week in flowing sea water in the laboratory tidal aquarium. (This method assumed that chitons would clear a similar area per rasp on perspex as they would on rock.) In December 1982, 10 chitons of different sizes were grazed overnight on the cultured algae plates held in the tidal aquarium. The plates were then rinsed with tap water, dried, and the size of cleared areas was measured using a stereoscopic microscope fitted with a micrometer eyepiece. The cleared areas were nearly elliptical, so the equation, $A = \pi ab/4$, where a and b are the longest and shortest axes of the cleared areas, was used to calculate the area A. The most prominent tooth on each side of the radula (the third lateral) appeared to do most of the rasping and, consequently, each side of the radula creates a cleared area. Hence, area A was doubled to give the area cleared per rasp. At least 30 rasps per individual were used to calculate a mean area cleared, and this area was related to animal length (Zeldis and Boyden, 1979).

The mean radular rasping rate (based on three 30 second periods of continuous rasping) was determined using the microphonic sensor described previously (section 2-3)

(Boyden and Zeldis, 1979). At least 12 animals of different sizes were used on each occasion. Size-related radular rasping rates were obtained for the high-shore group at water temperatures of 12, 14 and 17°C, and for the low-shore group at temperatures of 9, 12, 14, 17, and 18°C. These values covered the annual range of sea water temperatures experienced by chitons in the field.

The food energy on the substratum available to the chitons was estimated each month by collecting a minimum of six rocks from both low- and high-shore habitats. These were dried and a known area (between 21,000 and 30,000mm^2) of their surfaces was scraped lightly with a blunt knife. Scrapings were taken from the upper and lower surfaces of all rocks. The amount of organic matter in the scraped material was determined by ashing, and this value was converted to organic matter available per unit area of substratum. Bomb calorimetry of the monthly scraped material was prone to large error due to the small proportion of organic matter it contained (5-13% organic) and the problems of endothermy (Paine, 1966). However, samples from March, June, August and December from both high and low shores were bombed in an attempt to determine whether the calorific value of surface scrapings differed seasonally.

I assumed that marine diatoms made up the major component of the organic portion of the scrapings. Reported calorific values of diatoms are rare, but three values are available; 22.9 J mg^{-1} ash-free (Paine and Vadas, 1969), 20.6 J mg^{-1} ash-free (calculated from Platt and Irwin, 1973), and 23.0 J mg^{-1} ash-free (calculated from data giving mean proportions of carbohydrates, proteins and fats in diatoms by Parsons *et al*, 1961, and Platt and Irwin, 1973). Detritus, the assumed lesser component of the organic portion, would have been algal in origin, but have a slightly lower calorific content than diatoms due to leaching of nutrients. Based on these considerations, I took the organic portion of the scrapings to have a calorific value of 21 J mg^{-1} ash-free. This value is probably a satisfactory compromise between diatoms with at most 23 J mg^{-1} and detritus with at least 18 J mg^{-1} (the value of cellulose, Southwood, 1978). Seasonal variations in diatom calorific values have not been investigated previously, but studies on marine algae

show significant variation of this kind to be rare (Paine and Vadas, 1969; Mann, 1972; Himmelman and Carefoot, 1975).

Total consumption by each group was calculated using a computer programme (Appendix 1) that took into account monthly changes in both water temperature (and hence, in radular rasping rate) and population structure.

2-4-3 Growth Production (P_g)

Production of a population due to growth ($P_g = \Delta B + E$) is made up of two components: the change in non-gonadal biomass of the population resulting from growth and recruitment during the time in question (ΔB), and non-gonadal biomass lost as a result of mortality and migration (E) (Petrusewicz and Macfadyen, 1970). When all animals in a study area can be identified individually (as with homing limpets, e.g., Wright and Hartnoll, 1981) it is possible to measure accurately both these components at regular intervals. When individual identification is not possible, an equilibrium population for which the net annual change in biomass (ΔB) was zero, hence making P_g equal to mortality, is assumed (e.g., Hughes, 1971a,b). In my study, ΔB was measured once over a time interval of one year.

In January 1982, the body lengths of chitons were measured in 33 randomly placed $1 m^2$ quadrats at the high-shore site and in 6 quadrats at the low-shore site. This process was repeated in January 1983, this time sampling 50 high-shore and 15 low-shore quadrats. Regression lines relating body length to dry weight of somatic tissue calculated in November and December 1981 for both groups were used to convert these quadrat measurements into chiton biomass. As the shell-valves of chitons also contain organic matter in the form of protein and chitin (Hyman, 1967), this was estimated by dissolving the inorganic components of the valves from 30 chitons of known body length in dilute HCl and weighing the dried residue (Hughes, 1970). Shell-valve organic matter was assumed to have an energy content of 23.9 kJ g^{-1} (Paine, 1971). Total energy content of chiton somatic tissue, including shell organics, per square metre was calculated and the difference between the values obtained in 1982 and 1983 was taken as ΔB.

The elimination (E) component for the high-shore

group comprised a positive value due to mortality and a negative value due to immigration. Mortality was estimated by monitoring a group (initially 52) of homing chitons that were marked with scratches on their shell-valves. The proportion of animals missing after one year was used to estimate high-shore mortality rate. Annual mortality and immigration combined were estimated for the high-shore group from the smoothed length-frequency histograms for January 1982 and January 1983 divided into age-classes (e.g., all chitons between 20 and 25.6mm in length were designated age-class 2, all those between 25.6 and 31mm as age-class 3, and so on). The size intervals for each age-class were obtained from the growth equation (section 2-2). The change in area between age-class x in 1982 and age-class $x+1$ in 1983 gave an estimate of the net annual change in biomass attributable to mortality and immigration for chitons of that age. By summing over all age-classes, a mean value for E on the high-shore was obtained.

E for the low-shore group comprised two positive values: mortality and emigration. Monitoring individual low-shore animals in the field for a year was not possible, so E was estimated using the method of changes in area under the smoothed length-frequency histogram, as already described for the high-shore group.

2-4-4 Reproductive Production (P_r)

Sypharochiton pelliserpentis usually spawns once a year (Johns, 1960). Therefore, if the calorific value of gonads after spawning is deducted from that before spawning, annual P_r for each chiton group can be determined. To describe the reproductive cycle of *S. pelliserpentis*, the gonads of at least 35 chitons were examined each month, and the mean percentage of shell-free dry body weight made up by gonad (the gonad index) was calculated for males and females. The calorific value of male and female gonad was measured once in each of four stages of the cycle (pre-spawning, January; spawning, March; spent, May - August; development, October - December) to establish whether these values fluctuated seasonally.

Some reproductive production is lost through mortality and this component was estimated by taking the mean annual gonad index, multiplying by the mean biomass of the group,

then multiplying by the previously obtained mortality proportion (section 2-4-3). This procedure assumed that mortality occurred consistently throughout the year.

The relationship between animal size and gonad index for males and females was examined to determine whether larger animals contributed relatively more to P_r than smaller ones.

2-4-5 Respiration (R)

Aquatic respiration was measured at five temperatures (9, 11, 13.5, 15.5, 18°C) using individuals collected when the sea water temperatures were at the experimental temperature (September, June, May, April, February). On each occasion, 15 chitons covering the size range of animals at each site were collected from the shore just before the tide would have immersed them. They were taken to the laboratory and placed singly in 500ml glass jars with airtight screw tops. Sea water, which filled the glass jars completely, had already been equilibrated to the chosen experimental temperature and was maintained at this temperature (±0.1°C) throughout the 6h of an experiment. Dissolved oxygen was measured with the Winkler technique (Strickland and Parsons, 1972) and the difference in oxygen content between an experimental jar and the control jar (no chiton) was taken to be the oxygen used by the chiton.

Respiration in air was measured using compensating respirometers (Southwood, 1978). Six temperatures (5, 9, 13.5, 17, 21.5, 27 ±0.1°C) which covered the range experienced by most of the animals in the field were used, and measurements were again taken at the appropriate time of year (July, September, May, March, January, February). In each month, at least 13 chitons of various sizes were collected from the shore just after emersion, taken to the laboratory and placed singly in respirometer chambers. Oxygen uptake was recorded at 20 minute intervals for a minimum of 2h, after which measurements were averaged and used to calculate oxygen consumption on on hourly basis.

Animals with shell-valves free of epizoites were used in all respiration experiments. However, control tests using shell-valves removed from living chitons were run to check for microbial or algal respiration, with five sets of

valves being tested both in water at 15°C and air at 17°C. Results indicated that less than 2% ($\bar{x}$=0.3%, n=10) of live animal respiration was attributable to epizoites, and no corrections were made. Two trials were run to test for differences between day and night respiration, one in water at 18°C and the other in air at 21.5°C.

Total oxygen consumed by each chiton group was calculated using a computer programme (Appendix 1) that took into account monthly changes in population structure and temperature. The weight:respiration regression line used in any particular month was that obtained at the experimental temperature closest to the mean monthly air or water temperature (e.g., in May the mean air temperature was 12.3°C so the aerial respiration curve obtained at 13°C was used).

Metabolic energy output in J ml^{-1} O_2 at STP was calculated by multiplying oxygen consumed by an animal during respiration by an oxycalorific coefficient of 19.9. To select a suitable oxycalorific coefficient, RQ values (the proportion of CO_2 evolved to O_2 used) for four chitons were measured in May at 13°C in compensating respirometers (Southwood, 1978) and gave a mean value of 0.81 (s=0.01), indicating a coefficient of about 20.0 J ml^{-1} O_2 (Brody, 1945; Southwood, 1978). An oxycalorific coefficient of 19.8 J ml^{-1} O_2 was calculated on the assumption that chitons consumed mainly diatoms with an average chemical composition of 34.2% carbohydrate, 55.6% protein and 10.2% fat (Parsons *et al*, 1961; Platt and Irwin, 1973), and that the energy equivalents (Q_{ox}) of these three compounds were 21.1, 19.1 and 19.6 J ml^{-1} O_2, respectively (Elliott and Davison, 1975). The coefficient of 19.9 J ml^{-1} O_2 at STP was the mean of the two calculated values.

2-4-6 Defaecation (F)

It was not possible to collect the entire faecal production of an individual over a tidal cycle in the field. However, chitons would feed in the laboratory and the discrete, cylindrical faeces (Bandel, 1974) could be collected. At two-monthly intervals, at least 80 chitons were taken from the shore and divided into groups comprising 4 to 9 individuals of about the same size. They were allowed to adhere to a rock recently removed from their

habitat (one group per rock), and each rock was placed in a 2*l* plastic container with a hole covered by a 0.25mm mesh gauze in its base. The containers were covered with 1.5mm mesh gauze and placed on racks in the tidal aquarium at a height where the chitons experienced typical periods of immersiom and emersion as determined from field observations. Air and water temperatures in the aquarium closely approximated ($\pm 2^{o}C$) those in the field. The gauze-covered hole in the container base ensured that water could flow in and out, but that faeces were not lost. Each trial was run for two days; faeces were collected at each simulated low tide and dried to constant weight. Body lengths of all experimental animals were obtained, and the mean length of animals in each container was regressed against the mean dry weight of faeces produced per animal per day. Energy and ash contents of faeces were determined for each two-monthly sample to establish whether these values fluctuated seasonally.

Annual production of faeces by the high- and low-shore chiton groups was calculated using a computer programme (Appendix 1) that took into account monthly changes in population structure, defaecation rates and faecal calorific value.

2-4-7 Exudates (U)

U has been ignored in calculating most mollusc energy budgets as it has been assumed to be insignificant (e.g., Hughes, 1971a,b). Excreted ammonia was measured by Wright and Hartnoll (1981), and other workers have balanced their budgets by assuming that the difference between measured absorption (P+R) and expected absorption (C-F) was made up by production of nitrogenous excreta and mucus (e.g., Paine, 1971; Carefoot, 1967a). Miller and Mann (1973), however, suggested that the discrepency between measured and expected absorption could be attributed to a loss of dissolved organic matter (DOM) resulting from passive loss through body surfaces, loss from the anus with faeces or leached from faeces, loss from material being chewed, as well as active excretion. In the present study, production of mucus and two components of DOM were investigated as follows.

To estimate mucous production, 9 chitons of different

sizes were placed individually on pre-weighed glass plates, and the distance they moved was recorded. The plates were then rinsed with distilled water, air dried and re-weighed. No measurable weight gain (i.e., >0.1mg) was recorded in eight of the nine trials. However, it was noted that chitons which were removed from the substratum after being stationary for several hours had secreted a thin mucous film, particularly near the pallial groove. Therefore, 12 chitons of different sizes (4 from the high-shore, 8 from the low-shore) were placed on pre-weighed microscope slides and their movement was restricted so they soon became attached firmly. After 8h, the animals were removed, and the slides were rinsed, dried and weighed. Increase in weight was assumed to represent dried mucus. The measurements were complicated, however, because some mucus clearly remained on the foot and in the pallial groove of each removed chiton. As this residue could not be scraped off for fear of including epithelial cells or gill filaments in the mucous sample, an arbitrary correction factor of x2 was applied to the quantity of mucus adhering to the slide. This corrected value was multiplied by three to give an estimate of mucous production over 24h. The calorific value of mucus was assumed to be 23.97 kJ g^{-1} dry weight (Calow, 1974), and as mucus is produced from assimilated components of total consumption, in this study it is treated as a component of production, defined as P_m (Edwards and Welsh, 1982).

To measure two components of DOM, chitons were collected in April, July and December from the shore just before tidal immersion and placed immediately into 230ml plastic pottles containing 200ml of aerated sea water. Large animals (length > 33mm) were placed singly in pottles, small animals (length < 20mm) were tested in groups of three, and medium sized animals (length 20-33mm) were placed in pairs. Animals making up each triplet or pair were approximately the same size. Chitons were removed from the pottles after 6h, and their shell-free dry weights were determined. Duplicate samples (0.2ml) of water from each pottle were taken to determine quantities of ammonia nitrogen and urea nitrogen by microdiffusion (Conway, 1947). Results obtained from analyses of sea water controls run simultaneously were subtracted from the experimental values. It was assumed

that the chitons could release DOM only when immersed, that is for a period of approximately 6h in each tidal cycle for high-shore chitons, and 10h for low-shore animals. Hence, the results obtained for the low-shore chitons were multiplied by 1.67 (=10/6), whereas high-shore results were unmodified in calculating energy budgets. Energy values used were those given by Elliott and Davison (1975), i.e., 24.86 J mg^{-1} ammonia nitrogen and 23.06 J mg^{-1} urea nitrogen.

This approach, while indicating losses of dissolved organic nitrogen and quantifying two individual nitrogenous compounds, left some components unidentified and did not include any non-nitrogenous compounds. Unmeasured DOM was likely to be a small component of the total budget (Edwards and Welsh, 1982), but it must be kept in mind that values for U are underestimations.

3. RESULTS

3-1 Physical Data

The mean monthly sea water temperatures at the New Wharf, and air temperatures and sunshine hours at the meteorological station, are shown in Fig. 4. Air and water temperatures reached their maximum in February and minimum in July. Sea water temperatures were 1-2 degrees lower than average during the period from June to October, but otherwise the annual pattern was similar to previous years.

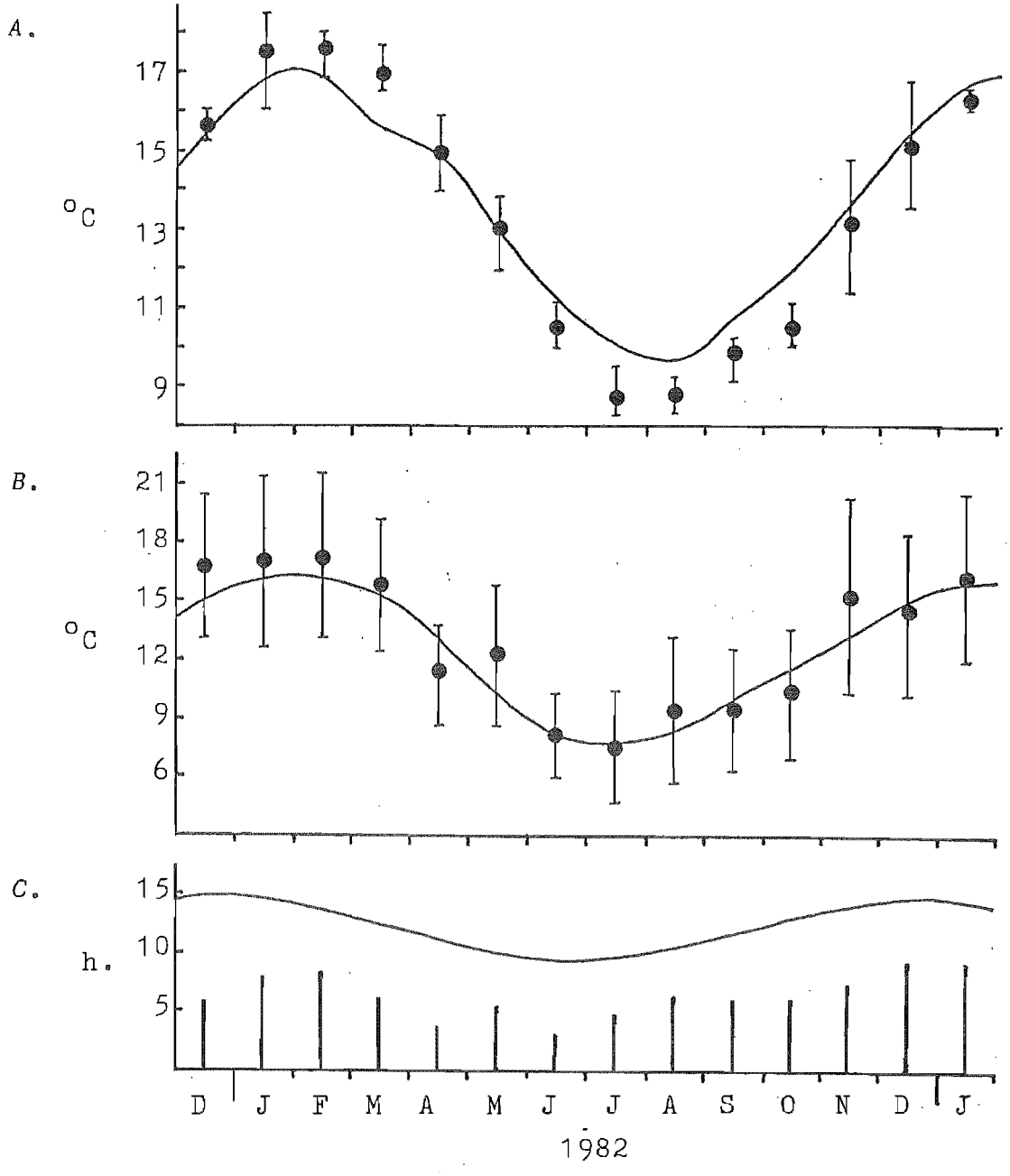


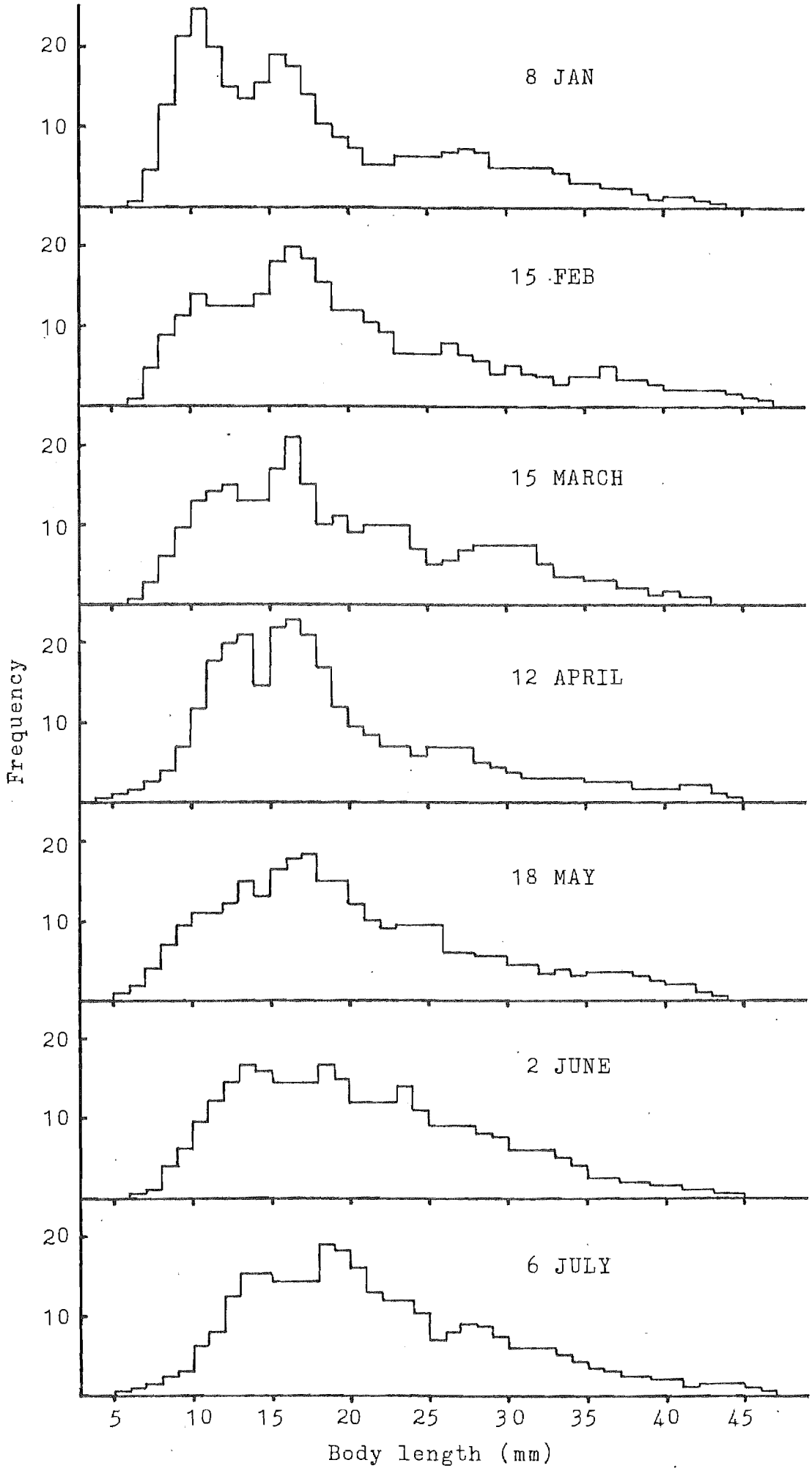
Fig. 4 - Physical data. *A*. Mean monthly sea water temperatures (± monthly range) recorded at New Wharf; solid line is mean water temperature curve calculated from data collected during 1962-64 (Rasmussen, 1965) and 1978-81 (EPFS records). *B*. Mean monthly air temperatures (± mean maximum and mean minimum) recorded at Kaikoura meteorological station; solid line is mean air temperature curve calculated from data collected over the period 1964-80 (from Kaikoura meteorological station). *C*. Mean daily sunshine hours recorded at Kaikoura meteorological station; solid line shows time between sunrise and sunset.

3-2 Population Structure

Length-frequency histograms are presented for both the low-shore (Fig. 5) and high-shore (Fig. 6) groups. The age structure of the low-shore group was strongly biased in favour of animals less than 25mm long; in January 1983, the mean shell-free dry weight of animals in this group was 162mg. Mortality appeared to be relatively high and few chitons attained a length greater than 45mm. Growth of the two smallest low-shore cohorts (which were identified by peaks at 11 and 16mm in the length-frequency histogram for January 1982) was followed until January 1983 when their median sizes were 16.5 and 21mm, respectively (Fig. 5). Annual growth increments of 5.5mm in the second year and 5mm in the third year correlated well with expected growth increments obtained from the calculated growth curve (Fig. 7). It was not possible to identify positively individual cohorts of animals older than three years because of the slow and variable growth of older *Sypharochiton*. It is important to note the virtual absence of a year 0 cohort (i.e., those chitons spawned about March 1982) in January 1983. Annual variations in recruitment success were suggested by a previous study of *S. pelliserpentis* (Horn, 1981), and it appears that the recruitment in 1982 was only about 15% of that which occurred the previous year.

The mean shell-free dry weight of high-shore chitons in January 1983 was 395mg, significantly greater than the mean low-shore weight (t-test, $P<0.01$). A high proportion of animals grew to at least 37mm, and chitons longer than 50mm were not uncommon.

Growth of both chiton groups was described by the Bertalanffy growth equation. The calculated constants for low-shore chitons were L_∞ = 48.74mm, L_0 = -0.81mm and K = 0.197 (Fig. 7), and for high-shore chitons they were L_∞ = 49.45mm, L_0 = 0.45mm and K = 0.245 (Fig. 8). Measured annual growth increments of five low-shore individuals monitored in a tidal aquarium, and six high-shore chitons monitored on the shore, are plotted also on Figs 7 and 8; their growth agreed well with the calculated growth curves.


8 JAN
15 FEB
15 MARCH
12 APRIL
18 MAY
2 JUNE
6 JULY
Frequency
20
10
5
10
15
20
25
30
35
40
45
Body length (mm)

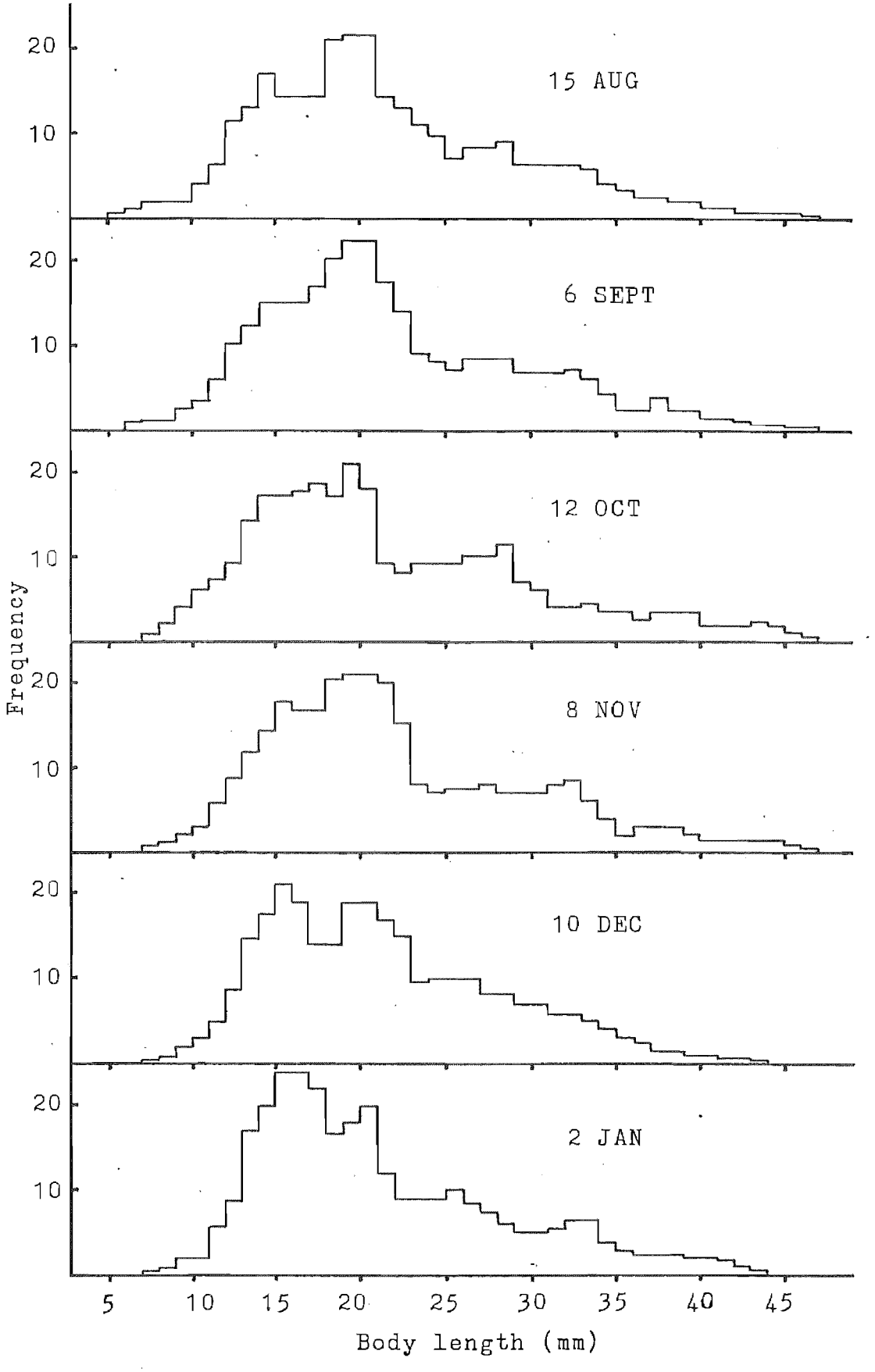
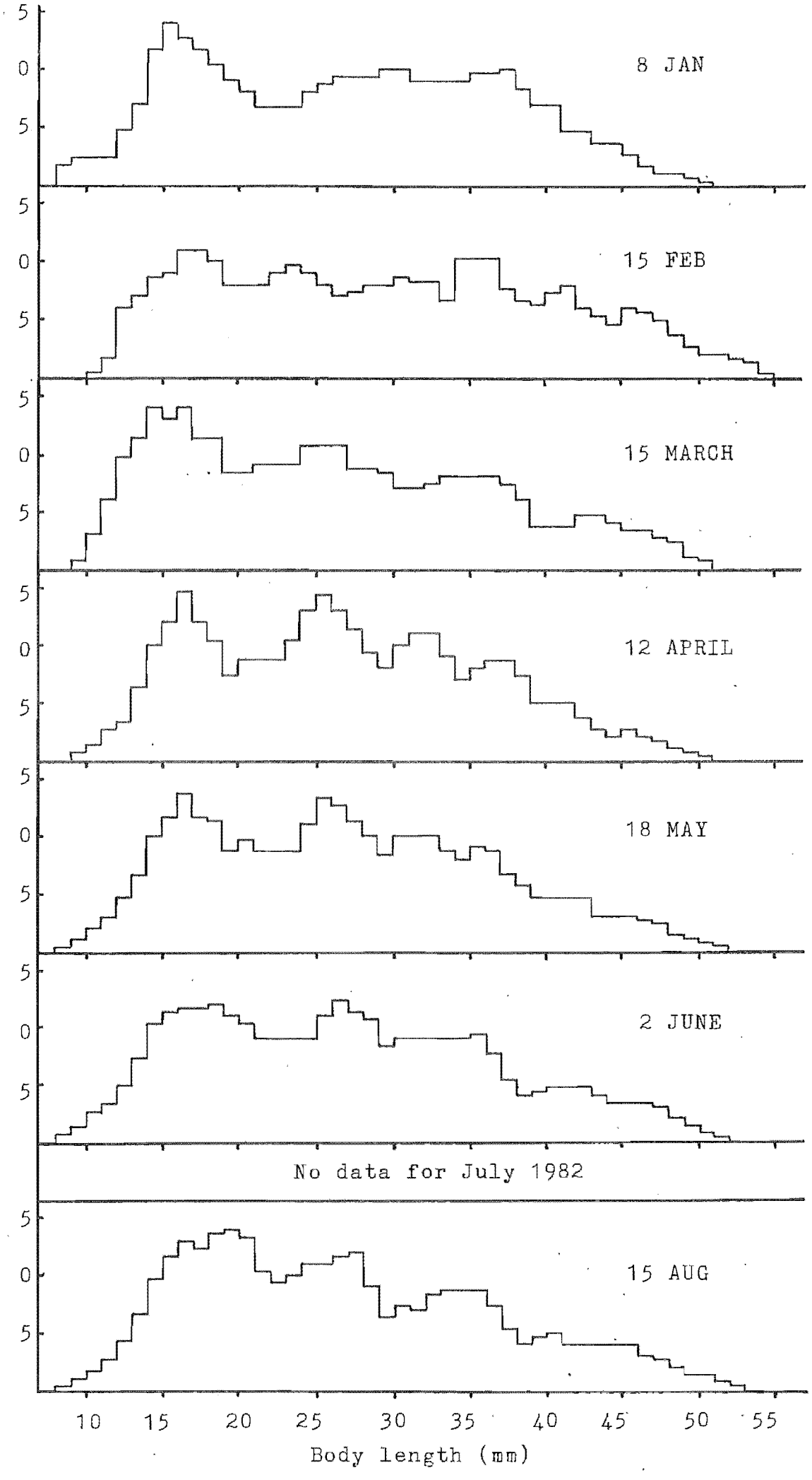


Fig. 5 - Length-frequency histograms for the low-shore chiton group recorded monthly over the period January 1982 to January 1983; n=300 for each histogram.


8 JAN
15 FEB
15 MARCH
12 APRIL
18 MAY
2 JUNE
No data for July 1982
15 AUG
10 15 20 25 30 35 40 45 50 55
Body length (mm)

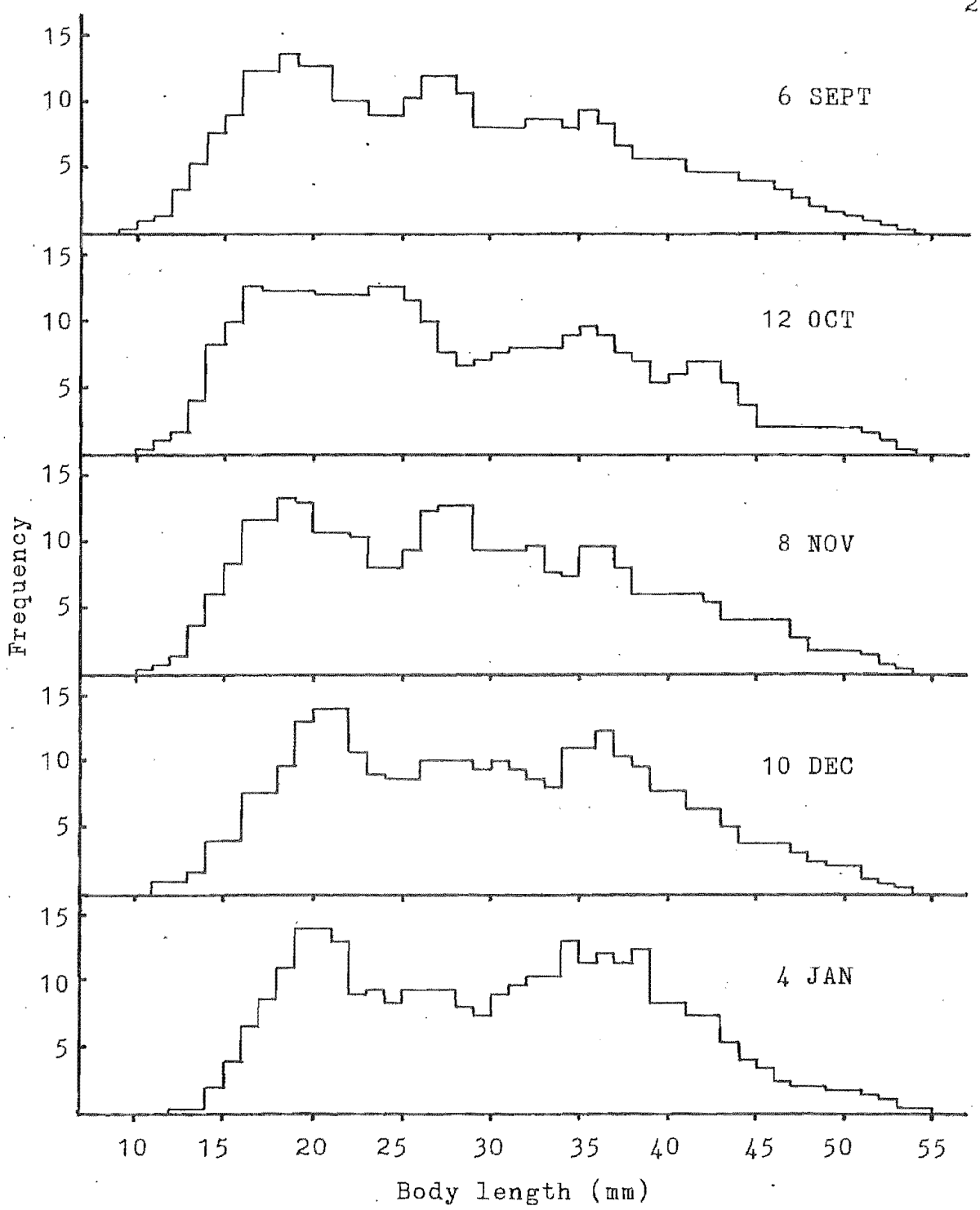


Fig. 6 - Length-frequency histograms for the high-shore chiton group recorded monthly over the period January 1982 to January 1983; n=300 for each histogram.

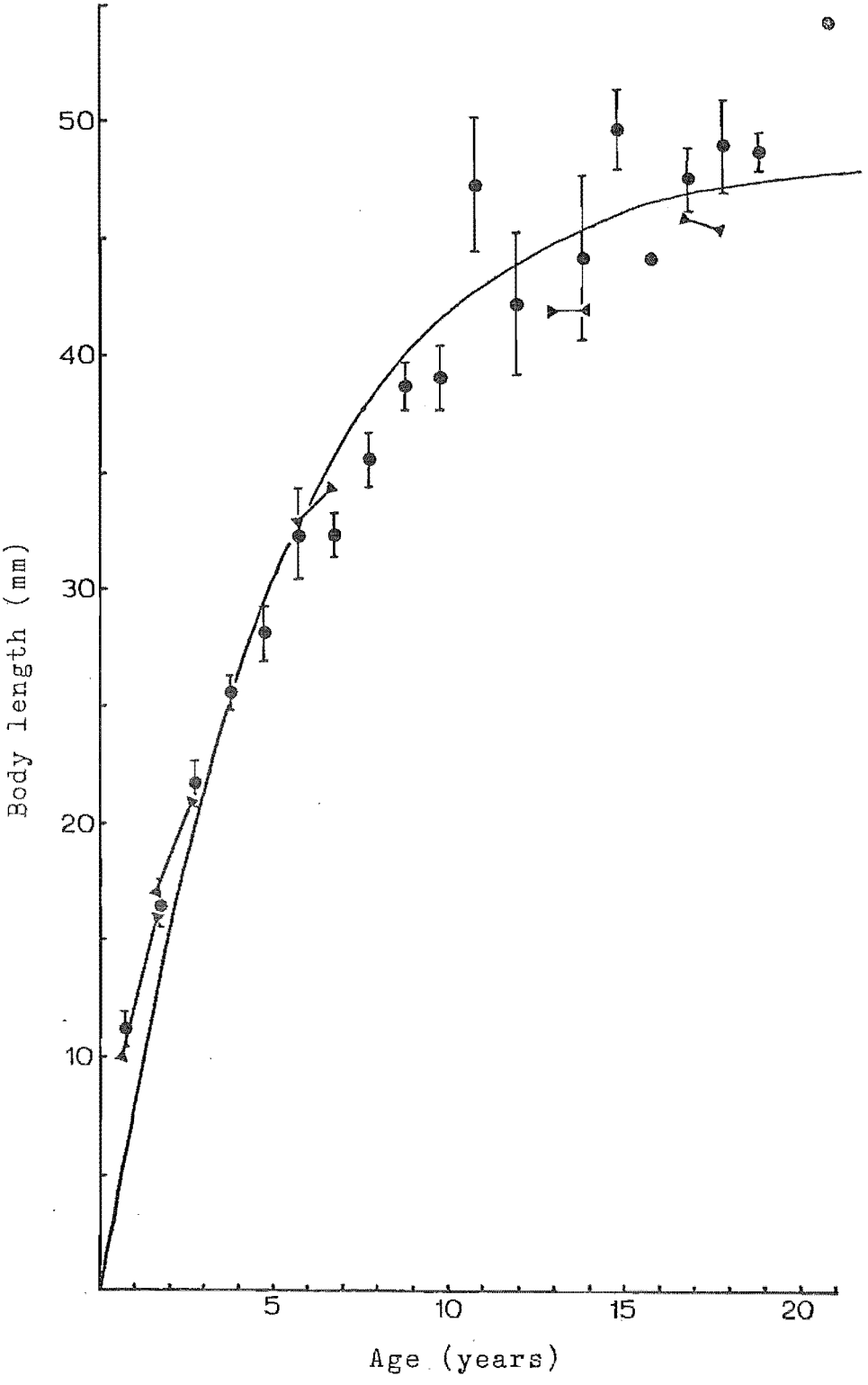


Fig. 7 - Growth curve of low-shore chitons, predicted by the Bertalanffy growth equation, fitted to data of body length means (± S.E. except where $n<3$) of each year-class. Annual growth increments of five monitored individuals are shown also (▶——◀).

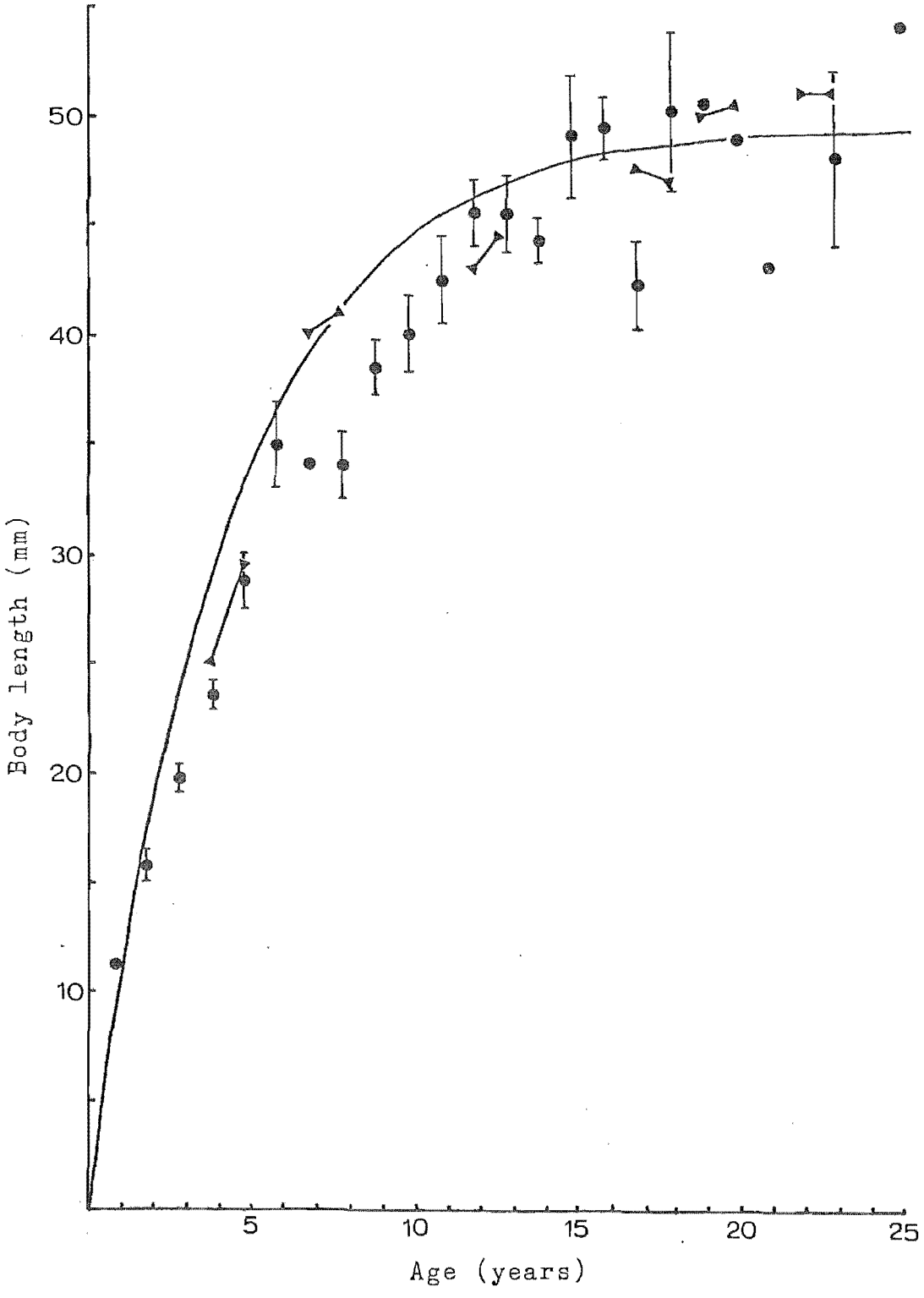


Fig. 8 - Growth curve of high-shore chitons, predicted by the Bertalanffy growth equation, fitted to data of body length means (± S.E. except where $n<3$) of each year-class. Annual growth increments of six monitored individuals are shown also (▶——◀).

3-3 Activity Patterns

Activity pattern data showed that high-shore chitons fed exclusively at night, usually when immersed, although some fed also when emersed on wet rock (Table 1). On average, high-shore chitons fed for close to 4.8h each day, although this time could be up to an hour longer in winter and an hour less in summer due to seasonal changes in night length. Each day, high-shore chitons moved during approximately 50% of their 11.5h immersion time, and 13% of their 12.5h emersion time (8.7h on dry rock, 3.8h on wet rock). Most chitons moving during daylight or on emersion appeared to be returning to their home sites rather than feeding.

Table 1 - Activity patterns for high-shore chitons showing the proportions (as a percentage of a sample of *n* chitons) that were moving and feeding, (nd = no data).

Situation	Month	Daylight			Darkness		
		n	Moving	Feeding	*n*	Moving	Feeding
Immersed	Jan	20	5	0	20	95	80
	April	25	4	0	21	90	76
	July	28	7	0	nd	-	-
	Oct	21	5	0	26	93	77
		$\bar{x}$	5.3%	0%	$\bar{x}$	93%	78%
Emersed on wet rock	Jan	25	4	0	28	38	7
	April	25	0	0	25	38	8
	July	25	0	0	nd	-	-
	Oct	25	0	0	25	40	8
		$\bar{x}$	1%	0%	$\bar{x}$	39%	8%
On dry rock	Jan	25	0	0	25	0	0
	April	25	0	0	25	0	0
	July	25	0	0	25	0	0
	Oct	25	0	0	25	0	0
		$\bar{x}$	0%	0%	$\bar{x}$	0%	0%

Low-shore chitons fed for about 5.6h each day and it seems probable that the length of this feeding period did not vary much seasonally, as approximately equal numbers of low-shore chitons fed in daylight and darkness (Table 2).

Most feeding occurs during immersion. Low-shore chitons move during approximately 80% of their 19h immersion time and 33% of their 5h emersion time (4h on wet rock, 1h on dry rock).

Table 2 - Activity patterns for low-shore chitons showing the proportions (as a percentage of a sample of *n* chitons) that were moving and feeding, (nd = no data).

Situation	Month	Daylight			Darkness		
		n	Moving	Feeding	*n*	Moving	Feeding
Immersed	Jan	30	80	27	27	78	30
	April	20	80	25	20	85	25
	July	35	77	26	nd	-	-
	Oct	29	76	23	22	77	27
		$\bar{x}$	78%	25%	$\bar{x}$	80%	27%
Emersed on wet rock	Jan	38	41	8	30	40	10
	April	37	42	11	25	48	12
	July	34	32	6	21	48	14
	Oct	39	28	8	30	53	13
		$\bar{x}$	36%	8%	$\bar{x}$	47%	12%
On dry rock	Jan	50	0	0	35	0	0
	April	49	0	0	33	3	0
	July	44	2	0	33	0	0
	Oct	50	0	0	20	0	0
		$\bar{x}$	0.5%	0%	$\bar{x}$	1%	0%

During the three months for which complete data are available (January, April, October), high-shore chitons fed during 72.9% (s=1.14) of the time they were moving, whereas animals from the low-shore spent a significantly shorter portion ($\bar{x}$= 32.3%, s= 2.45) of their active period feeding (t-test, $P<0.001$). It appears, therefore, that high-shore chitons exhibit a behavioural adaptation which enables them to maintain an adequate level of consumption in the face of a shorter period when feeding can occur.

3-4 Energy Budget

3-4-1 Consumption (C_m)

Most species of chiton feed by scraping a mixture of rock particles and encrusting organisms into the mouth (Boyle, 1977). *Sypharochiton* showed no evidence of food selectivity, and this appears to be typical of chitons that feed primarily on microscopic films of algae and diatoms (e.g., Glynn, 1970; Demopulos, 1975). However, it was clear from examination of faeces and field observations of grazing animals, that *Sypharochiton* not only fed on diatoms and detritus scraped from the rock surface but also on macroalgae. Occasionally, faeces of high-shore chitons contained stems of the complanate form of the brown alga, *Scytosiphon lomentarius*, particles of *Corallina officinalis* and fragments of *Ulva* sp. (when it bloomed on the high shore in late winter and spring). Sometimes, faeces of low-shore chitons contained the encrusting or turf forms of *C. officinalis*. Occasionally, I observed in the field, low-shore chitons feeding directly on *Corallina* turf and also on *Hormosira banksii*; however, on none of the occasions when activity pattern data were collected, was more than one of the minimum of 20 observed animals feeding on macroalgae. Hence, probably less than 5% of feeding time is spent in that activity. It was assumed that the consumption of macroalgae did not change the calculated calorific values of consumption significantly. It was not possible to make comparisons of rock surface and macroalgae on an "energy per bite" basis as only area (and not volume) cleared per radular rasp could be calculated.

In both chiton groups, radular rasping rate increased with increasing temperature, and decreased with increase in body size. These relationships were best expressed by the following equation:

$$R = -0.224L + (1.795T - 2.394),$$

where R = radular rasping rate (rasps per minute), L = body length (mm), and T = temperature (^{o}C). The equation was calculated by taking the mean slope (= -0.224) of the five regression lines relating body length and radular rasping rate obtained at different temperatures (Fig. 9), and regressing temperature against the intercept (a) of each of those five lines ($a = 1.795T - 2.394$).

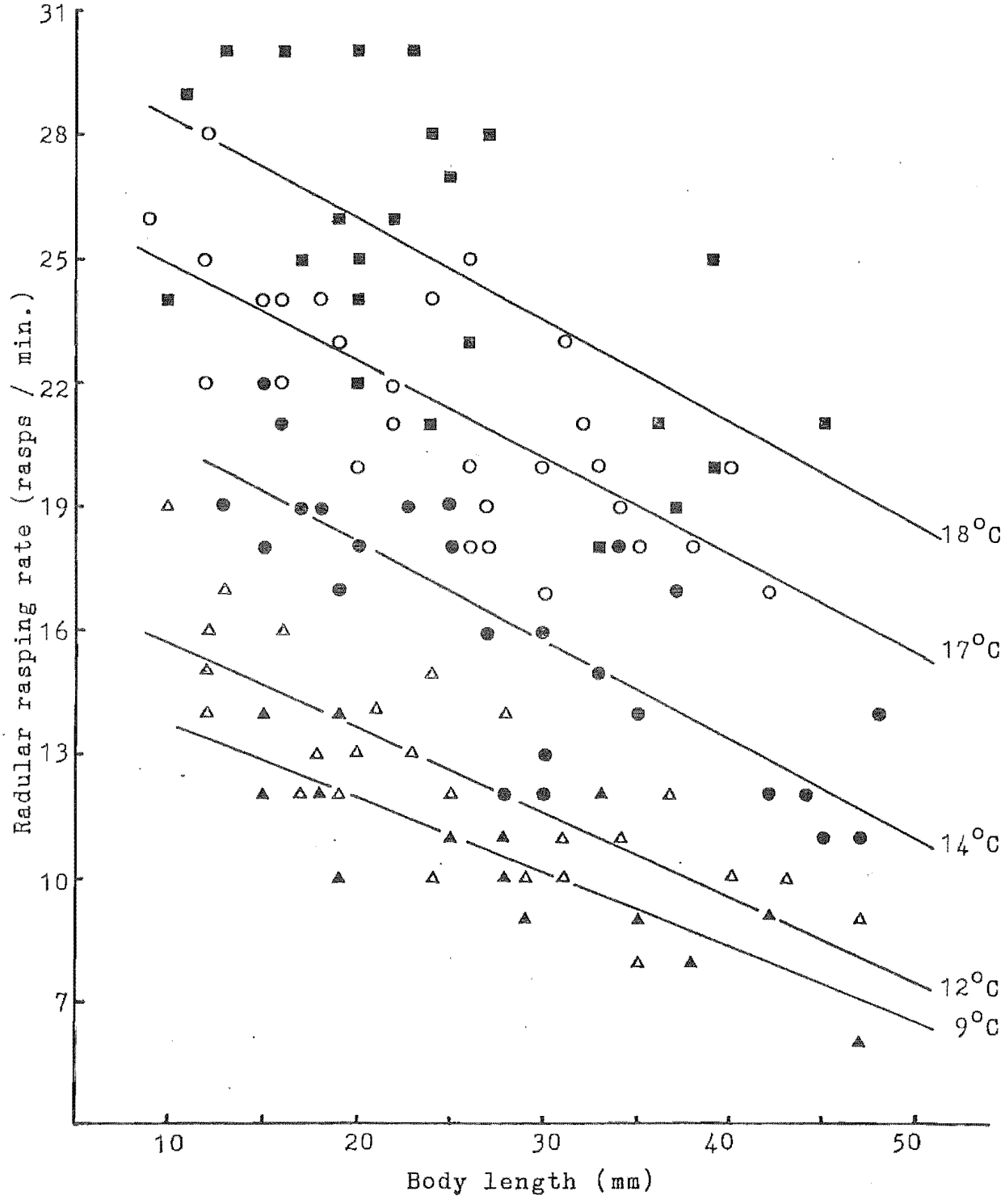


Fig. 9 - Radular rasping rate (rasps per minute) of chitons from the high- and low-shore groups combined, measured at five different temperatures (■ 18°C, O 17°C, ● 14°C, △ 12°C, ▲ 9°C). Correlation coefficients (r) of regression lines range from 0.68 to 0.91.

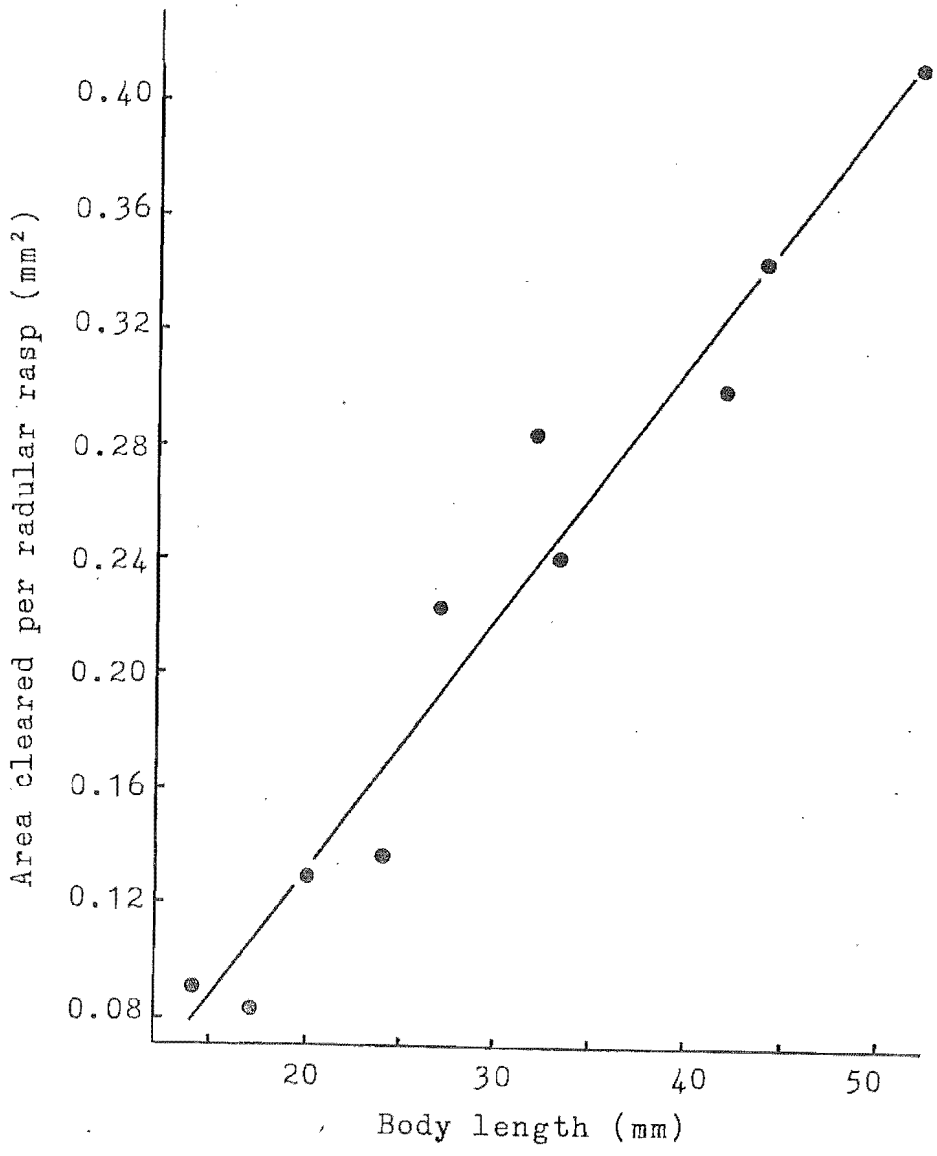


Fig. 10 - Relationship between body length (L) and area cleared per radular rasp (A), (overlapping of cleared areas has been taken into account, see text for details); equation of line is $A=0.0088L-0.044$ ($r=0.977$; S.E. <0.007 mm^2 for all points).

Comparisons of high- and low-shore rasping rates were made at three temperatures (12, 14 and 17°C). However, ANCOVA showed no significant differences between groups (all $P>0.05$), although there was significant difference between data at different temperatures. Hence, data obtained at similar temperatures on both shores were combined on Fig. 9.

Area cleared per radular rasp was related linearly to chiton body length (Fig. 10). Consecutive rasps by chitons frequently resulted in the overlapping of cleared areas, often by as much as 50%. The mean overlapped proportions

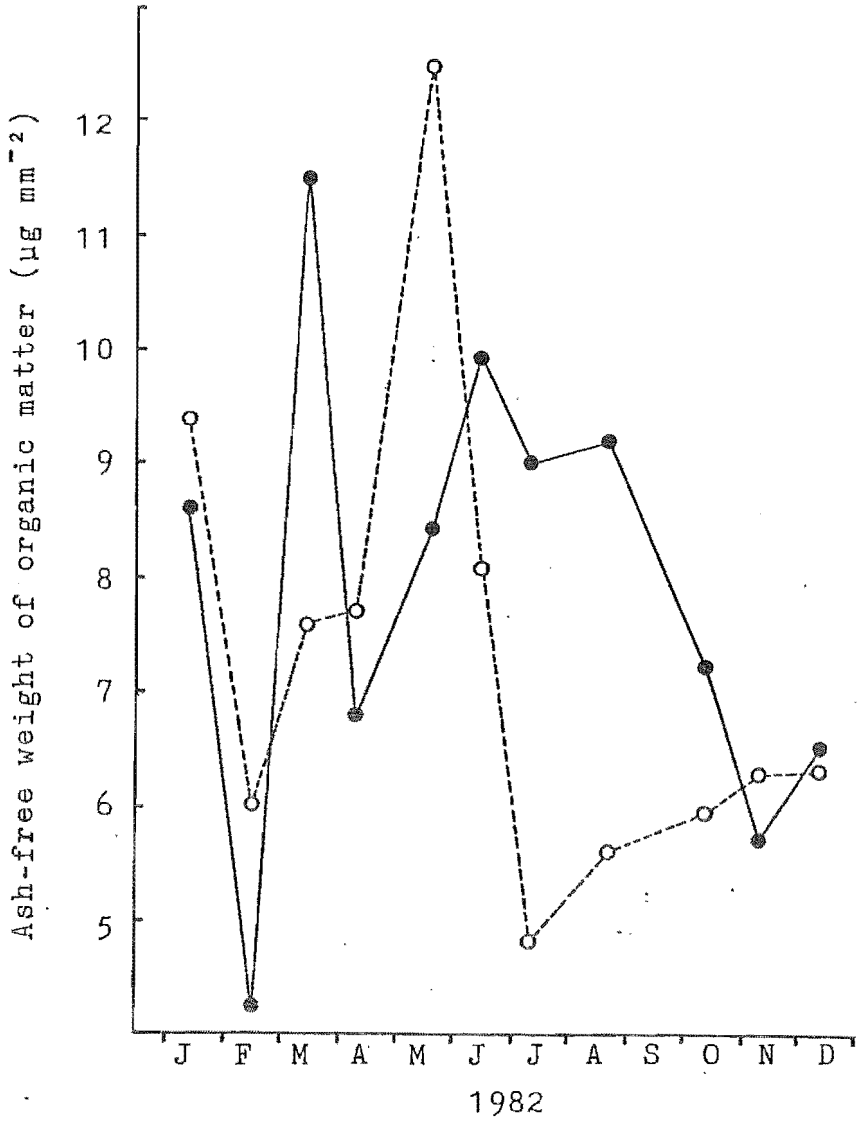


Fig. 11 - Organic matter available to grazing chitons on the low (●) and high (○) shores; each point obtained by ashing one rock scraping sample.

of 115 cleared areas was 30%, and this correction was applied to the cleared area data before calculation of the regression line in Fig. 10. This regression equation implied a negative exponential relationship between the weight-specific area cleared per radular rasp and dry tissue weight; e.g., a 13mm (0.04g) chiton cleared a surface area of 1.75mm^2 g^{-1} with each rasp, whereas a 45mm (0.77g) chiton cleared only 0.48mm^2 g^{-1}.

Biomass of ash-free organic matter on the high and low shores showed no clear seasonal trends (Fig. 11). Annual mean values (± standard deviations) were 7.30 (± 2.80) on the high shore, and 7.92 (± 2.07) µg mm^{-2} on the low shore, (not significantly different, t-test, $P>0.05$). Assuming a calorific value of 21 J g^{-1} organic matter, then 0.153 J mm^{-2}

and 0.166 J mm^{-2} were present on the high and low shores, respectively. The calorific value of stone surface organic matter was assumed to be equal at all times, as the results of bomb calorimetry on rock scrapings from high- and low-shore sites in March, June, August and December were not significantly different (*t*-test, $P>0.05$, $n=4$/site/month).

Calculated monthly consumption varied considerably throughout the year and was about three times higher in February (68 kJ m^{-2} and 212 kJ m^{-2} on the high- and low-shores, respectively) than in August (22 and 76 kJ m^{-2}, respectively). This variation was due mainly to differences in water temperature, and hence, in radular rasping rate, and also to changes in population structure. Total annual consumption (C_m) by the high-shore chitons was calculated to be 471.1 kJ m^{-2}, and for the low-shore group, 1521.1 kJ m^{-2}.

3-4-2 Growth Production (P_g)

The relationships between chiton body length and somatic tissue weight are listed in Table 3. These regression equations were used on all occasions when the conversion of one measured variable (length or weight) into the other variable was required.

The calorific value of somatic tissue of male and female chitons from both groups varied throughout the year. On the low shore, highest calorific values were recorded at the times of peak gonad index (January 1982 for males and females, and October for males only, see section 3-4-3) (Fig. 12). Calorific values declined to a minimum in May (after spawning), then immediately began to increase again. Female tissue generally contained about 500 J g^{-1} more energy than male tissue. On the low shore, somatic tissue calorific value and gonad index appeared to be inversely related (Fig. 13). Calorific values of male and female tissue declined to their lowest levels at the time of peak gonad index, steadily increased after spawning and during the resting phase, and began to decline again after the onset of gametogenesis.

The calorific value of immature animals (those for which sex could not be determined) (Table 4) was less than that of mature chitons (Figs 12 and 13). Hence, a mean value of 17.8 kJ g^{-1} ash-free was used in calculations of

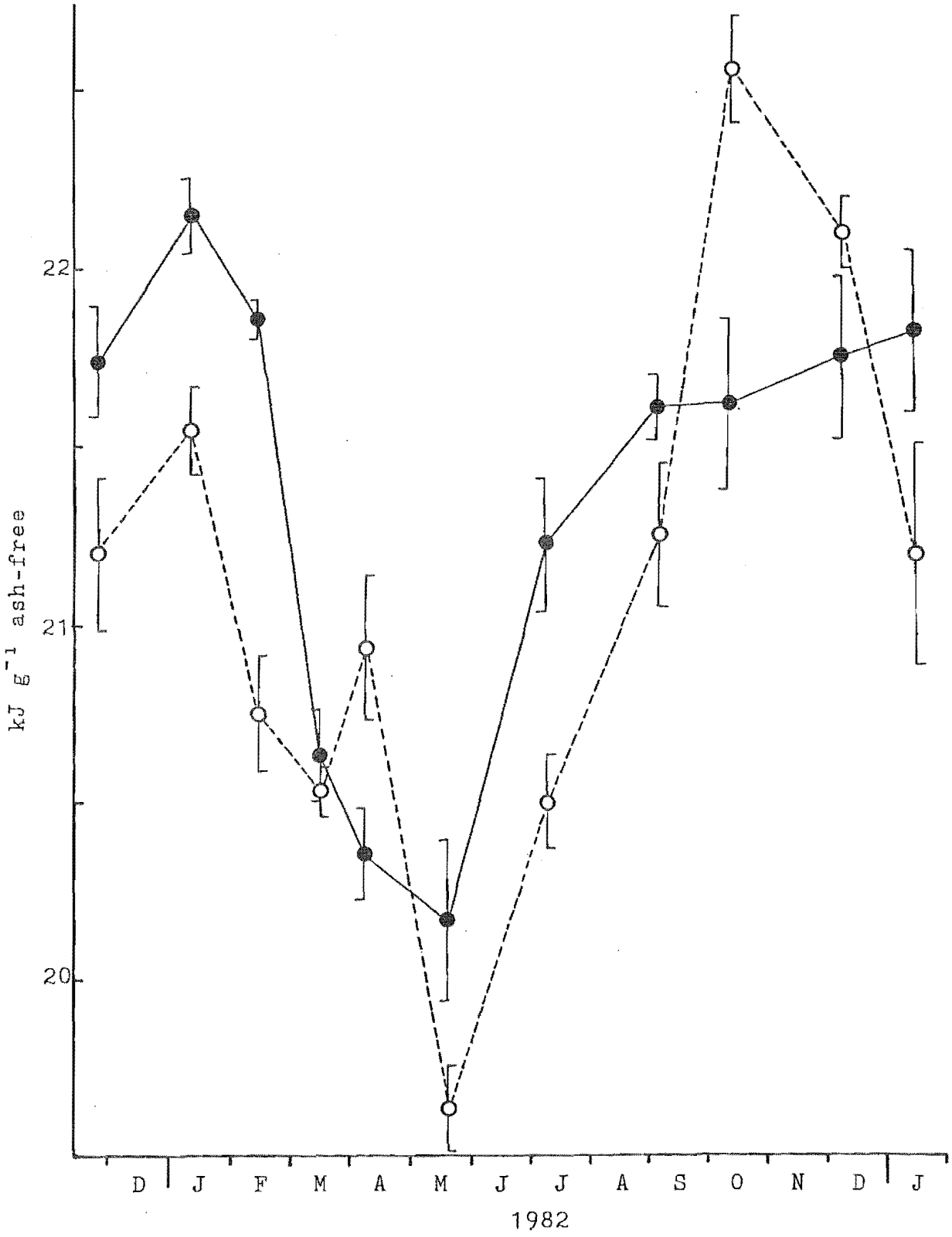


Fig. 12 - Calorific value (kJ g^{-1} ash-free) of male (O) and female (●) somatic tissue of high-shore chitons; ($\bar{x}$ ± S.E., n = 4 for each point).

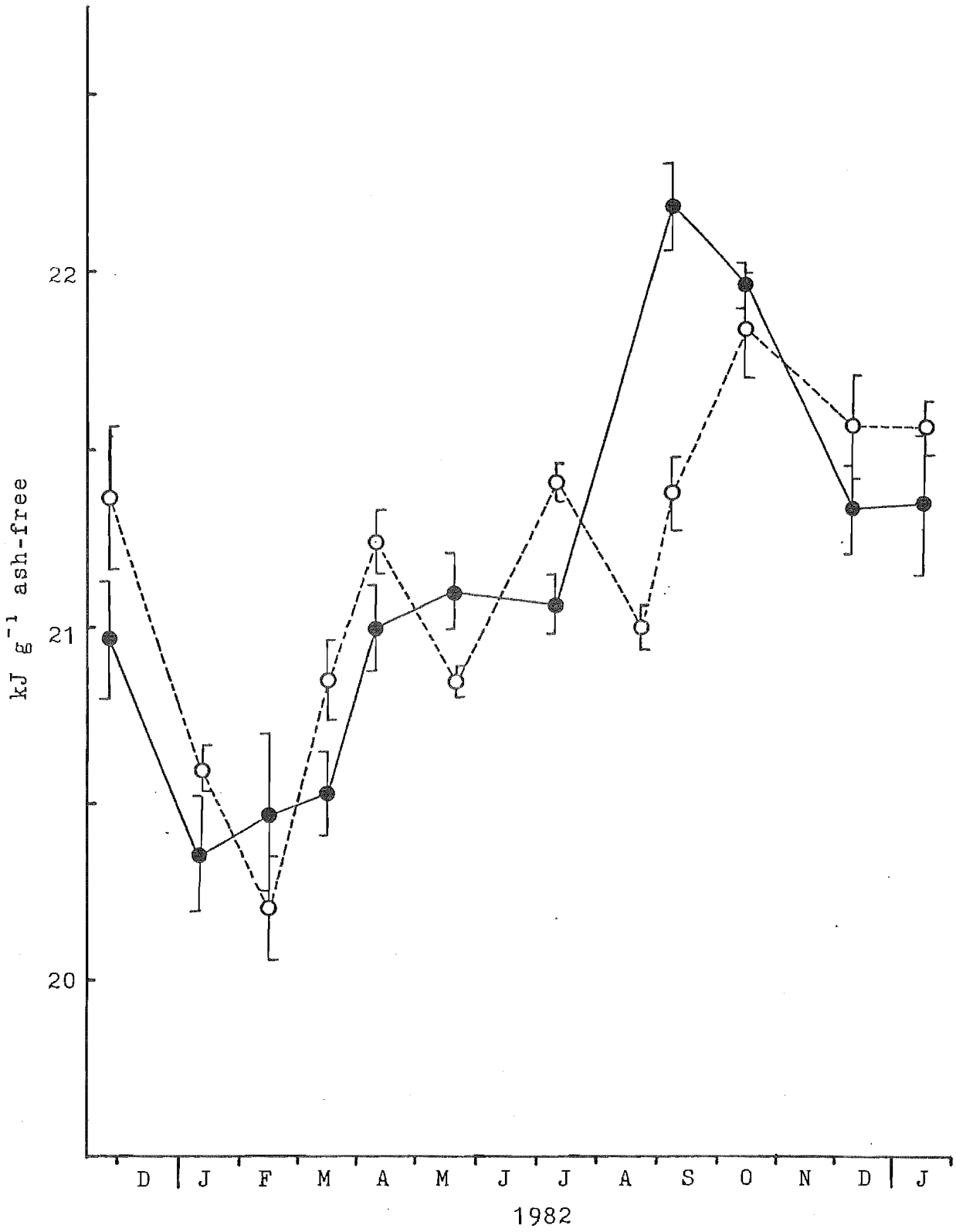


Fig. 13 - Calorific value (kJ g^{-1} ash-free) of male (O) and female (●) somatic tissue of low-shore chitons; ($\bar{x}$ ± S.E., n = 4 for each point).

P_g for all chitons less than one year old. (Most chitons could be sexed after 12 months.)

Some seasonal and inter-group variations in ash content of somatic tissue were apparent also (Fig. 14). Ash content was highest in January in both groups, but lowest values were recorded in May-July for low-shore chitons, and in August-October for high-shore chitons. Proportion of ash to total tissue weight was significantly higher each month (except May and July) on the low-shore (t-test, $P<0.01$).

Table 3 - Calculated relationships between chiton body length (L, mm) and three weight parameters; shell-free dry somatic tissue weight (W, g), dry weight of shell-valves (S, g), and dry weight of shell-valve organic matter (P, g).

Chiton group	Equation	n	r
High shore	$\ln W = 2.460 \ln L - 9.514$	55	0.975
Low shore	$\ln W = 2.381 \ln L - 9.249$	55	0.981
High & Low shore	$\ln S = 3.427 \ln L - 11.907$	105	0.982
High & Low shore	$\ln P = 0.0769 L - 6.234$	30	0.972

Table 4 - Calorific value and ash content of somatic tissue of immature chitons. (* = material sufficient for only one calorific determination, otherwise $n=4$. One determination of ash content per sample was made.)

Chiton group	Period	kJ g^{-1} ash-free ($\bar{x}$ ± S.E.)	% ash
High shore	March- July	17.50 ± 0.40	42.1
	Nov - Dec	18.14*	40.8
Low shore	Feb - July	18.11 ± 0.44	43.5
	Oct - Dec	17.31 ± 0.37	43.8

The relationships between body length, shell weight and shell organic weight (Table 3) indicate that shell organic weight is equivalent to about 10% of a chiton's dry somatic tissue weight. Therefore, this proportion was used in calculating the contribution of shell organics to P_g.

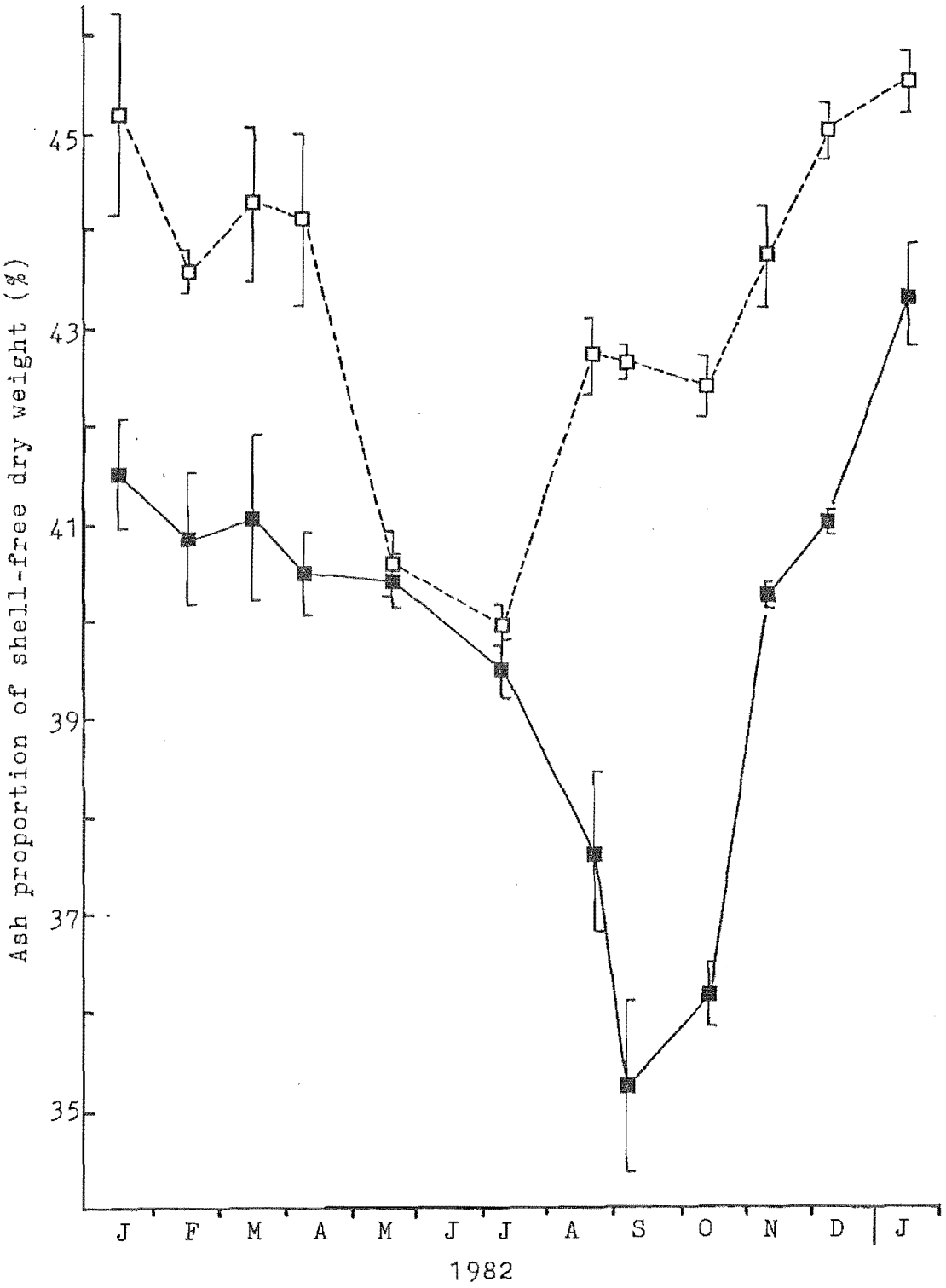


Fig. 14 - Variation in ash proportions of shell-free dry somatic tissue weight for high-(■) and low-shore (□) chitons; ($\bar{x}$ ± S.E., n = 3 for each point).

Data obtained from the quadrat surveys of chiton density in January 1982 and January 1983 are listed in Table 5. The high-shore group made a net biomass gain over this period, and mean animal size increased, despite a slight reduction in chiton density. The low-shore group suffered a net biomass loss as well as a substantial reduction in density, although mean animal size increased.

The ΔB component of P_g was calculated from the calorific values of mean dry weight of somatic tissue and shell organics per square metre in January 1982 and January 1983. On the high shore, the increase in somatic tissue amounted to 2.99 kJ m^{-2} , and that of shell organics to 0.32 kJ m^{-2}, giving a ΔB value of 3.31 kJ m^{-2} $year^{-1}$. On the low shore, ΔB was negative and comprised -6.98 kJ m^{-2} somatic tissue and -1.12 kJ m^{-2} shell organics, a total ΔB of -8.10 kJ m^{-2} $year^{-1}$.

The elimination (E) component of P_g for the low-shore group was calculated using change in area under a smoothed length-frequency histogram (Fig. 15). Estimates of mortality and emigration combined are listed in Table 6, and the mean value of 34.3% was taken as the proportion of chitons eliminated annually from this group. (It is interesting to note the relatively low elimination proportions for age-classes 0 and 1, suggesting a possible "refuge in size" for small chitons against predation.) The calorific value of somatic tissue lost was 39.82 kJ m^{-2}, and shell organic loss amounted to 4.51 kJ m^{-2}. This gave a total value for E of 44.33 kJ m^{-2} $year^{-1}$.

The E component of P_g for the high-shore group was calculated in a similar way using change in area under the smoothed length-frequency histograms shown in Fig. 16. Estimates of immigration and mortality are listed in Table 7, and the mean value of 22.9% was taken to be the annual mortality fraction. Immigration by animals in their first and second years clearly occurred. Older animals also may have migrated from the low to the high shore, but only in numbers considerably less than the number of high-shore chitons that died. A second estimate of high-shore mortality was obtained by monitoring 52 chitons on the shore. Ten of these animals disappeared during the year and their absence was interpreted as mortality, giving a mortality estimate of

Table 5 - Chiton density, total somatic tissue weight, and total shell organic weight, per square metre for the high- and low-shore chiton groups in January 1982 and January 1983. (Standard Deviations are given in parentheses.)

Chiton group	Date	No. of quadrats	Density (No. m^{-2})	Somatic tissue weight (g m^{-2})	Mean animal weight (g)	Shell organics (g m^{-2})
High shore	8-1-82	33	9.1 (9.0)	3.102 (3.486)	0.341	0.213
High shore	4-1-83	50	8.7 (8.9)	3.439 (3.694)	0.395	0.237
Low shore	8-1-82	6	34.8 (19.1)	5.058 (2.581)	0.145	0.377
Low shore	2-1-83	15	26.3 (17.3)	4.231 (2.596)	0.162	0.306

Table 6 - Estimate of elimination for the low-shore group using changes in area under length-frequency histograms. (Area = area under curve (Fig. 15) for each individual age-class, in arbitrary units; Elimination = mortality and emigration combined.)

1982 Age-class	Area	1983 Age-class	Area	Elimination (%)
		0	169	
0	1086	1	838	22.9
1	931	2	658	29.3
2	532	3	333	37.4
3	319	4	211	33.8
4	203	5	132	34.8
5	130	6	84	35.5
6	83	7	50	39.1
7	50	8	33	34.0
8	33	9	19	41.5
				$\bar{x}_{0-8} = 34.3$

Table 7 - Estimates of elimination for the high-shore group using changes in area under length-frequency histograms. (Area = area under curve (Fig. 16) for each individual age-class, in arbitrary units; * = mortality of 1982 age-classes 0 and 1 was assumed to be 22.9%, the mean value for all other age-classes.)

1982 Age-class	Area	1983 Age-class	Area	Immigration (%)	Mortality (%)
		0	0		
0	225	1	470	-131.8	22.9*
1	820	2	1126	-60.3	22.9*
2	763	3	671		12.0
3	709	4	548		22.7
4	564	5	483		14.4
5	437	6	338		22.7
6	330	7	230		30.2
7	200	8	142		29.2
8	137	9	88		36.8
9	83	10	66		21.0
10	63	11	52		17.5
					$\bar{x}_{2-10} = 22.9$

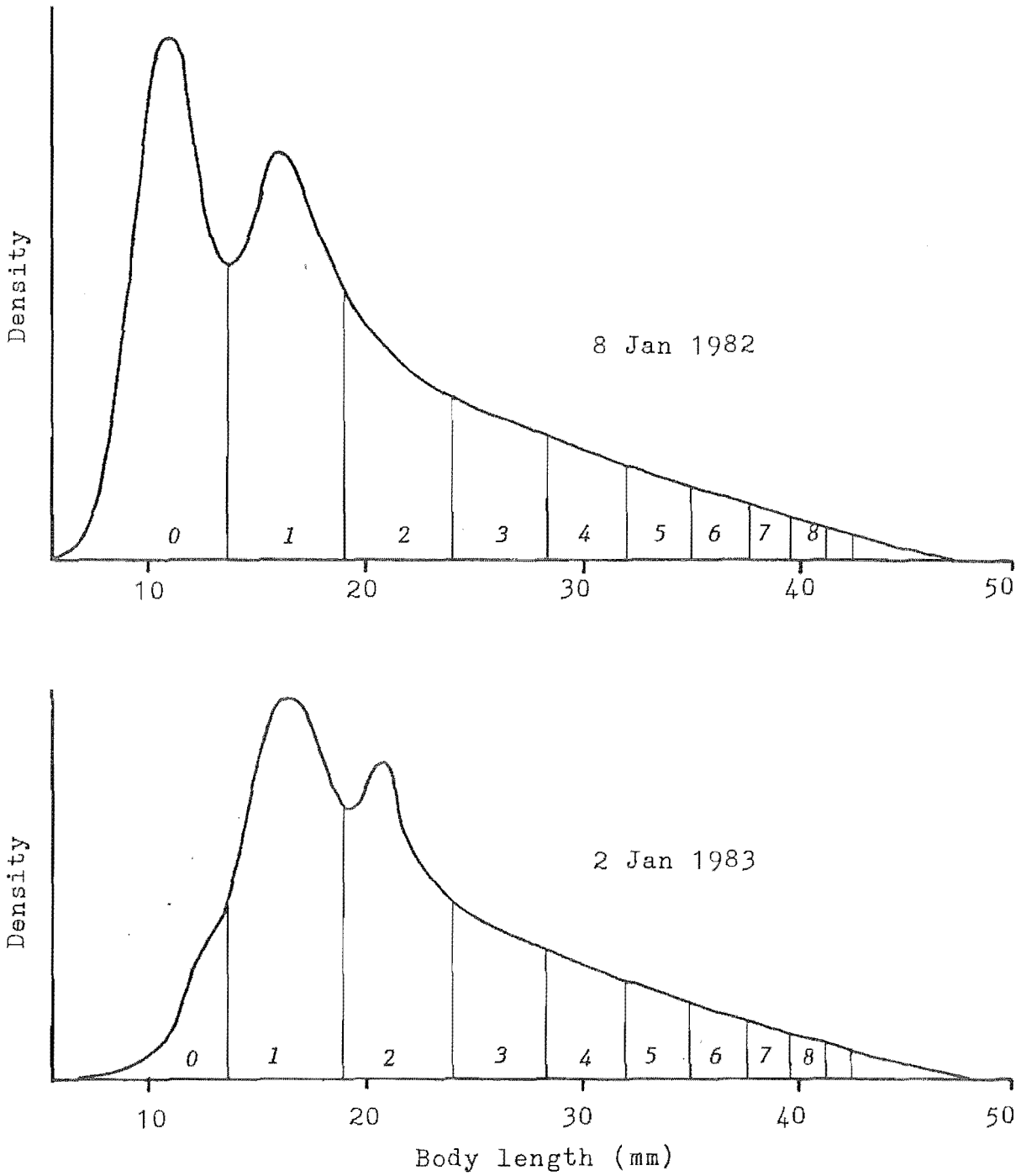


Fig. 15 - Smoothed length-frequency histograms for the low-shore chiton group in January 1982 and January 1983, divided into age-classes (using the calculated Bertalanffy growth equation). The difference between the area attributed to age-class x in 1982 and to age-class $x+1$ in 1983 was taken as an estimate of elimination.

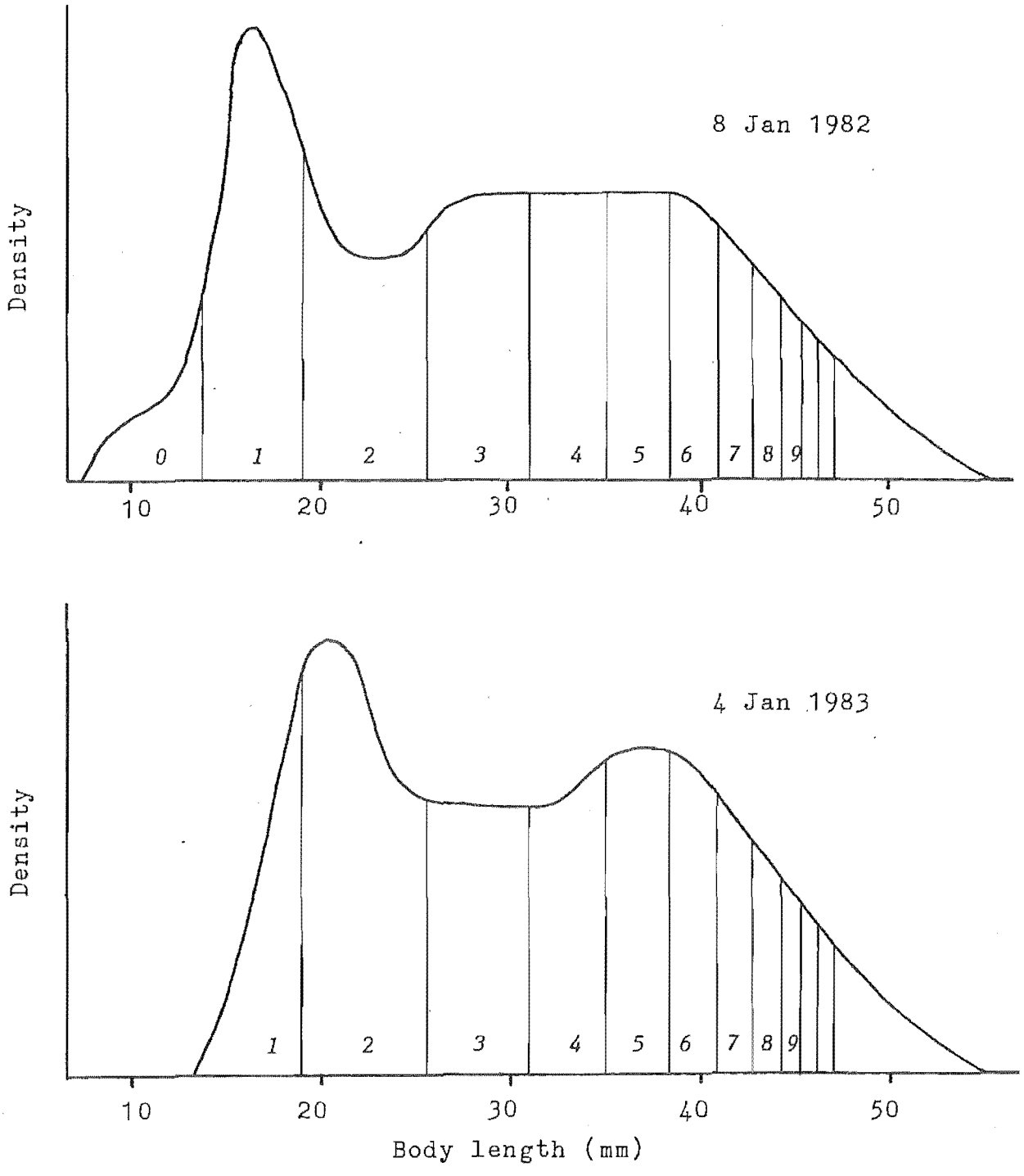


Fig. 16 - Smoothed length-frequency histograms for the high-shore chiton group in January 1982 and January 1983, divided into age-classes (using the calculated Bertalanffy growth equation). The difference between the area attributed to age-class x in 1982 and to age-class $x+1$ in 1983 was taken as an estimate of elimination.

19.2%. This latter value is very similar to that used in P_g calculations (22.9%) and obtained by analysing length-frequency histograms.

Hence, for the high-shore group, mortality accounted for 17.35 kJ m^{-2} (15.59 and 1.76 kJ m^{-2} for somatic tissue and shell organics, respectively) and immigration totalled -2.08 kJ m^{-2} (-1.88 and -0.20 kJ m^{-2} for somatic tissue and shell organics, respectively). Total E was 15.27 kJ m^{-2} $year^{-1}$, therefore.

Total growth production ($\Delta B + E$) was calculated to be 18.58 kJ m^{-2} $year^{-1}$ on the high shore and 36.23 kJ m^{-2} $year^{-1}$ on the low shore.

3-4-3 Reproductive Production (P_r)

The sex ratios of the two chiton groups were not significantly different from 1:1 (χ^2 test, $P>0.05$). Of 864 low-shore chitons, 53.5% were males and 46.5% females, whereas 47.7% of the 792 high-shore chitons were males and 52.3% were females. These percentages were used to estimate reproductive production.

The annual cycles of gonad indices (dry gonad weight as a percentage of dry tissue weight) are plotted for the high-shore (Fig. 17) and low-shore (Fig. 18) groups. Both sexes spawned simultaneously (late January on the high shore and late February on the low shore) and spawning was complete by early May. High-shore males released 6.5% of their dry body weight as gametes, and females 5.9%. Corresponding percentages for low-shore chitons were 7.9% and 5.0%. Calorific values of gonadal tissue at four distinct periods of the reproductive cycle are shown in Table 8. In high- and low-shore animals, the energy content of ash-free testes increased slightly with maturation, from 23.7 to 24.7 kJ g^{-1}, and 23.0 to 24.7 kJ g^{-1}, respectively. Ovaries exhibited a far greater calorific increase with maturation, from 24.3 to 26.8 kJ g^{-1} for high-shore, and 21.4 to 26.6 kJ g^{-1} for low-shore chitons. Gonad ash content also varied with season (Fig. 19). Ovaries were low in inorganic matter during development and high during the resting phase, whereas testes contained their lowest proportions of ash during resting and highest amount when mature.

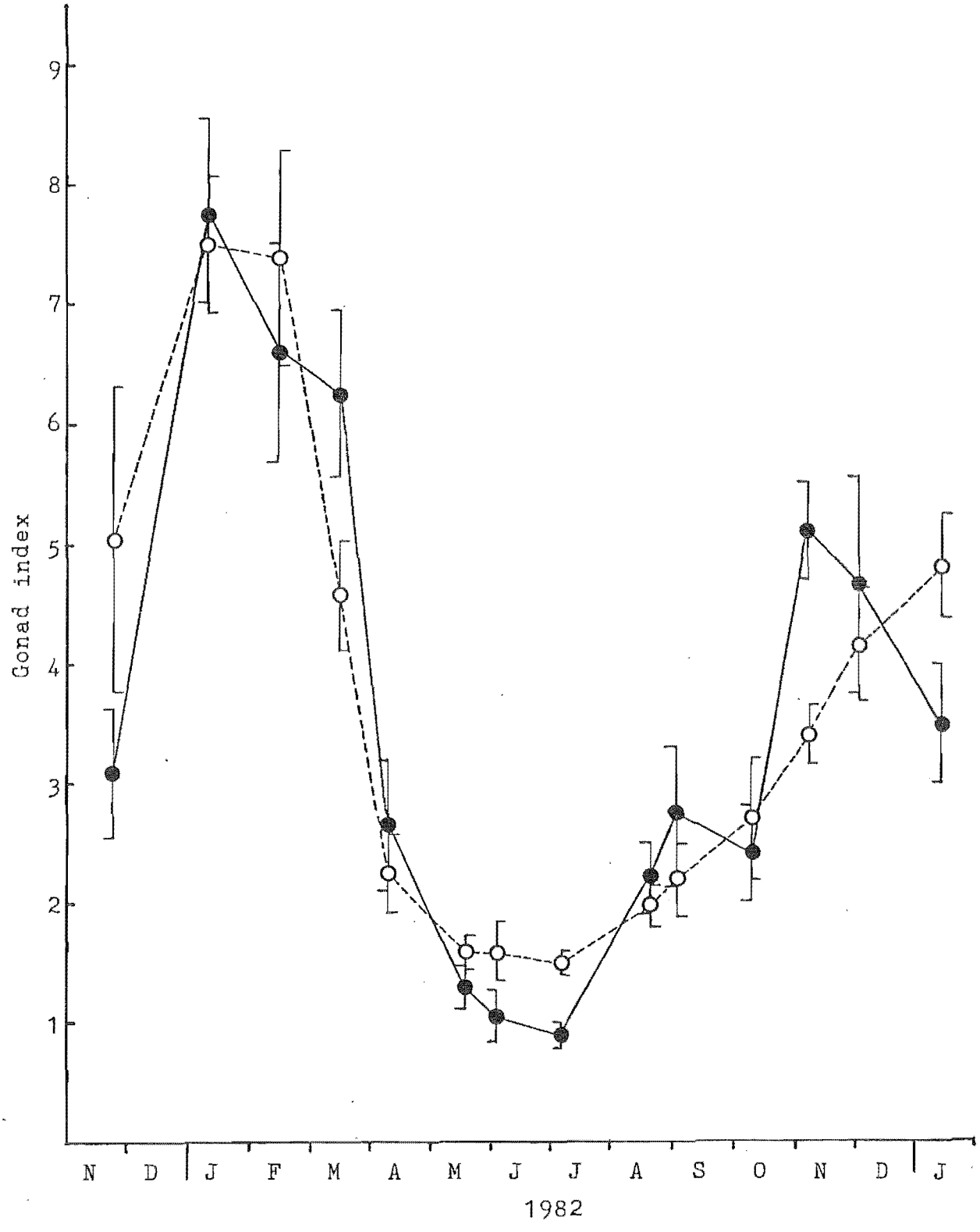


Fig. 17 - Gonad indices (percentage of total shell-free dry weight made up by reproductive tissue) for the high-shore chiton group, (● = Male, O = Female, $\bar{x}$ ± S.E.).

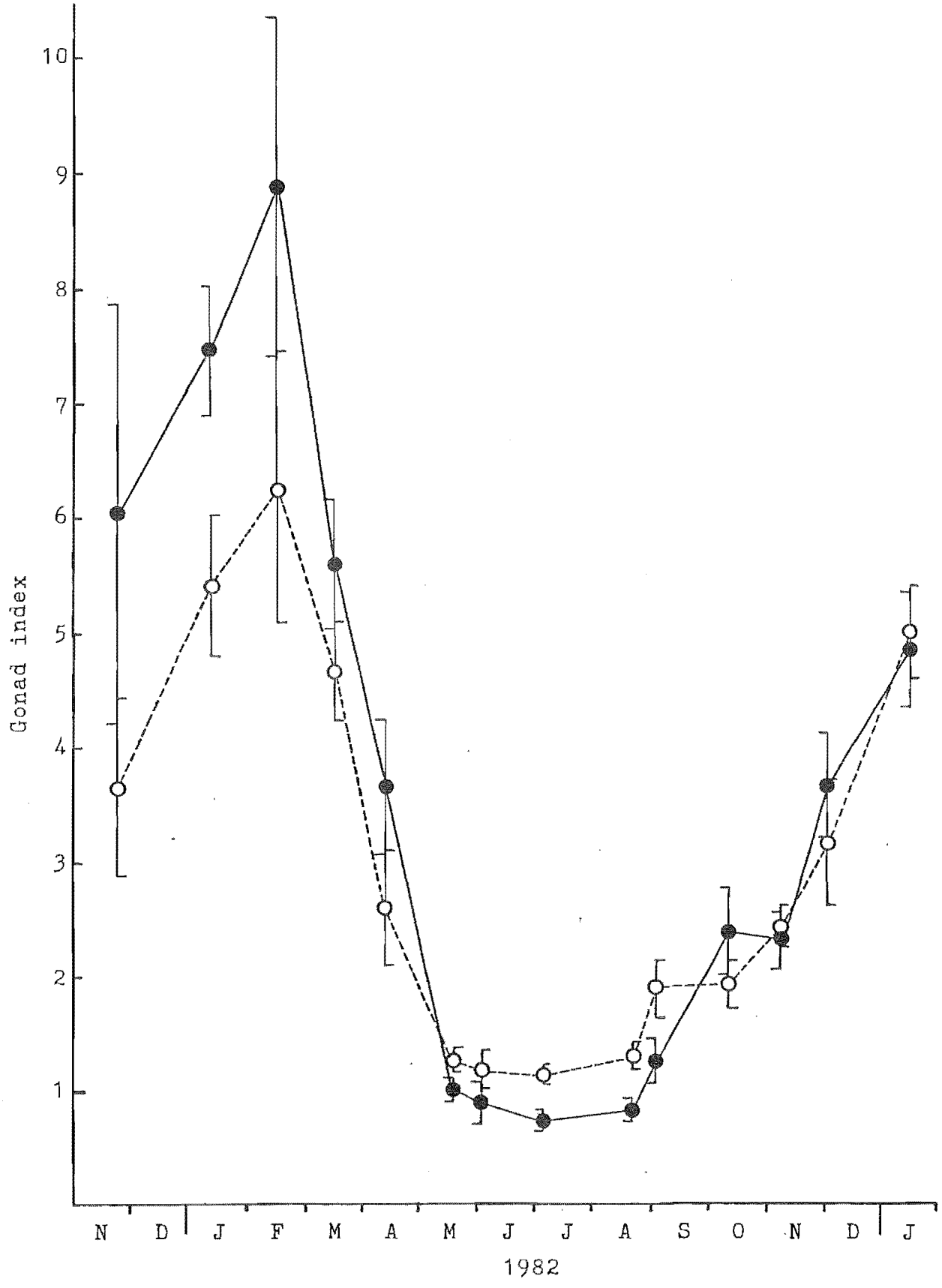


Fig. 18 - Gonad indices (percentage of total shell-free dry weight weight made up by reproductive tissue) for the low-shore chiton group, (● = Male, ○ = Female, $\bar{x}$ ± S.E.).

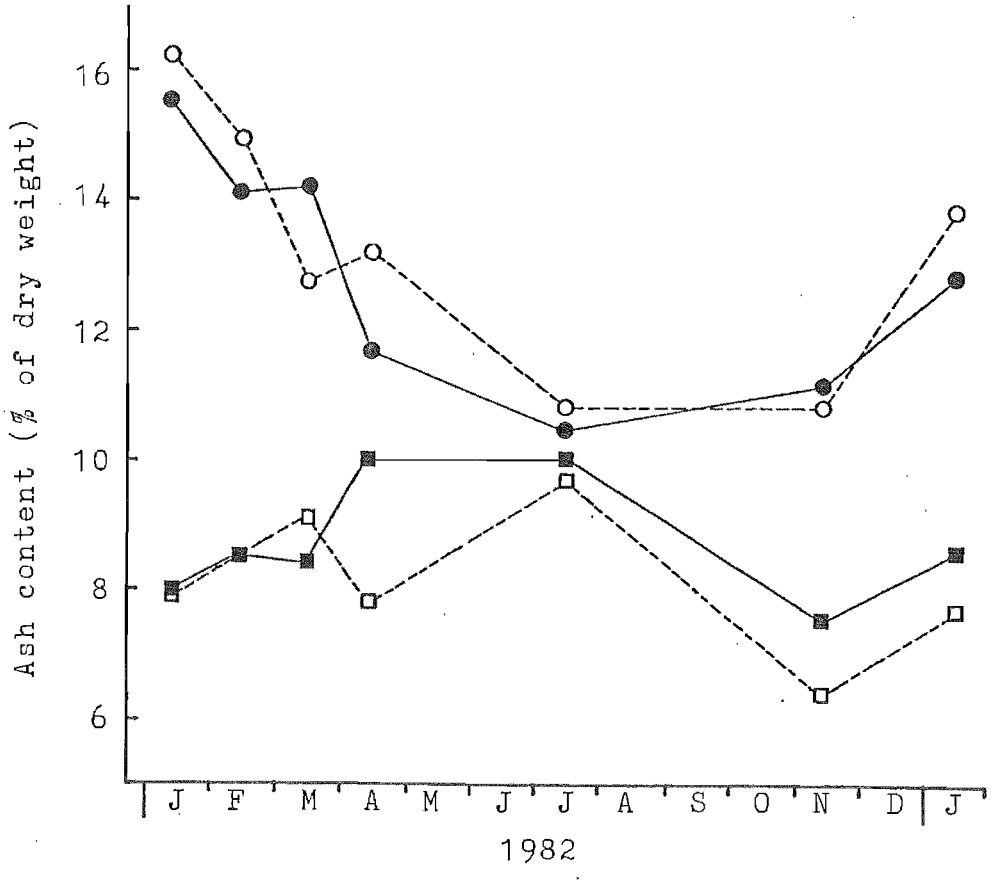


Fig. 19 - Ash content of gonad as a percentage of dry gonad weight plotted as a mean of two samples. July data are a combination of gonads collected from May to September, and data plotted in November comprise gonads from October to December. (● = High-shore male, ○ = Low-shore male, ■ = High-shore female, □ = Low-shore female.)

Reproductive production by each sex from both shore levels was calculated by taking the total somatic and gonad tissue at the time of spawning, multiplying that figure by the proportion of weight released as gametes, and multiplying that product by the calorific value of gametes at spawning. For example, for high-shore female chitons, the assumed somatic tissue per square metre at the approximate time of spawning (30 January) was 52.3% of 3.130g, plus 7.51% gonad (=1.760g), of which 5.9% was released as gametes (=0.104g), multiplied by the calorific value 24.33 kJ g^{-1}, giving a total of 2.54 kJ m^{-2}. Similarly, the value for high-shore males was 2.20 kJ m^{-2}, 2.94 kJ m^{-2} for low-shore females, and 4.64 kJ m^{-2} for low-shore males.

Reproductive production lost through mortality was calculated by taking the mean annual weight of somatic and gonad tissue, and multiplying by the mean gonad index, then

by the mean calorific value of gonad, and finally by the mortality fraction. For example, for high-shore female chitons, the mean somatic plus gonad tissue was 1.742 g m^{-2}, of which 3.4% was gonad (=0.059 g), multiplied by the mean calorific value 23.18 kJ g^{-1}, of which 22.9% was lost by mortality, giving a total of 0.32 kJ m^{-2}. Similarly, P_r lost through mortality for high-shore male chitons was 0.28 kJ m^{-2}, 0.48 kJ m^{-2} for low-shore female chitons, and 0.62 kJ m^{-2} for low-shore male chitons. Total P_r is shown in Table 9.

Table 8 - Energy values of gonads for January (immediate pre-spawning), March (mid-spawning), May to August (resting), and October to December (development). (The first value represents energy in kJ g^{-1} dry weight, the second is the standard deviation of that value, and the third is energy in kJ g^{-1} ash-free weight.) Each value is the mean of four replicates.

Chiton group	Period	Male		Female	
High shore	January	20.84 (2.51)	24.66	24.67 (1.73)	26.79
	March	21.08 (0.61)	24.58	24.33 (0.80)	26.58
	May-Aug	21.90 (1.43)	24.45	21.91 (1.83)	24.34
	Oct-Dec	21.03 (2.62)	23.67	23.69 (0.95)	25.62
Low shore	January	20.66 (0.55)	24.67	24.12 (1.91)	26.19
	March	20.54 (1.06)	23.54	24.17 (1.97)	26.60
	May-Aug	21.86 (0.97)	24.51	21.76 (0.68)	24.10
	Oct-Dec	20.55 (1.80)	23.05	22.80 (3.22)	24.35

Table 9 - Reproductive production, showing the contributions made by spawned gametes and gametes lost through mortality by both sexes from both chiton groups.

Chiton group	Contribution	Female	Male	Totals
High shore	Spawned gametes	2.54	2.20	4.74
	Mortality loss	0.32	0.28	0.60
	Total P_r			5.34 kJ m^{-2}
Low shore	Spawned gametes	2.94	4.64	7.58
	Mortality loss	0.48	0.62	1.10
	Total P_r			8.68 kJ m^{-2}

It is possible that larger chitons contributed relatively more P_r per gram body weight than smaller ones, as large animals often had gonad indices greater than the monthly means (the most extreme example being a male low-shore chiton with an index of 24.7% in February). Such a possibility was tested by regressing shell-free dry weight against gonad index for each month's data. The mean slopes and mean correlation coefficients were calculated from the regressions when gonads were either resting (April to September) or developing and spawning (January to March, and October to January) (Table 10). While the positive slopes suggest a relatively greater contribution by larger chitons, correlation coefficients were weak, suggesting no significant size-dependent variations in P_r; hence, no corrections were applied to this component.

Table 10 - Mean slopes (A) and mean correlation coefficients (r) of regression lines relating dry body weight to gonad index.

Chiton group & sex	Resting		Development/Spawning	
	A	r	A	r
High-shore male	1.96	0.555	3.08	0.486
High-shore female	1.86	0.497	3.07	0.541
Low-shore male	1.18	0.309	3.05	0.309
Low-shore female	1.57	0.436	1.79	0.272

The gonad cycle was monitored for 14 months, and it appeared that reproductive production in 1983 was going to be less than in 1982 (Figs 17 and 18). Comparison of gonad indices from January in both years showed that only the values for low-shore female chitons were not significantly different (t-test, $P>0.05$). The January 1983 indices for male and female high-shore, and male low-shore chitons were significantly less than the January 1982 values (t-test, $P<0.01$).

3-4-4 Respiration (R)

The relationship between oxygen consumption (R) and shell-free dry body weight (W) can be expressed as:

$$R = aW^b$$

where a is a proportionality factor and b is the weight exponent (Hemmingsen, 1960). This can be expressed linearly:

$$\log R = \log a + b.\log W.$$

The parameters of this regression for each set of measurements of aquatic and aerial respiration are listed in Table 11, and regression lines are plotted in Figs 20-23.

Table 11 - Parameters of the regression, $\ln R = \ln a + b.\ln W$ for each set of measurements of aerial and aquatic respiration. R = oxygen consumption at STP (ml h^{-1}), W = shell-free dry body weight (g), r = correlation coefficient of regression.

	Temp.	High Shore			Low Shore		
	(°C)	a	b	r	a	b	r
Aerial Respiration	27	0.134	0.645	0.985	0.156	0.405	0.930
	21.5	0.147	0.760	0.936	0.136	0.616	0.938
	17	0.123	0.784	0.959	0.102	0.654	0.941
	13.5	0.089	0.698	0.941	0.092	0.703	0.982
	9	0.072	0.875	0.978	0.087	0.877	0.960
	5	0.039	0.677	0.960	0.066	0.973	0.981
	$\bar{x}_{5-27}$		0.737			0.705	
Aquatic Respiration	18	0.120	0.682	0.976	0.140	0.559	0.938
	15.5	0.131	0.697	0.966	0.104	0.605	0.978
	13.5	0.106	0.670	0.960	0.103	0.652	0.973
	11	0.109	0.705	0.959	0.103	0.680	0.962
	9	0.097	0.690	0.964	0.085	0.738	0.982
	$\bar{x}_{9-18}$		0.689			0.647	

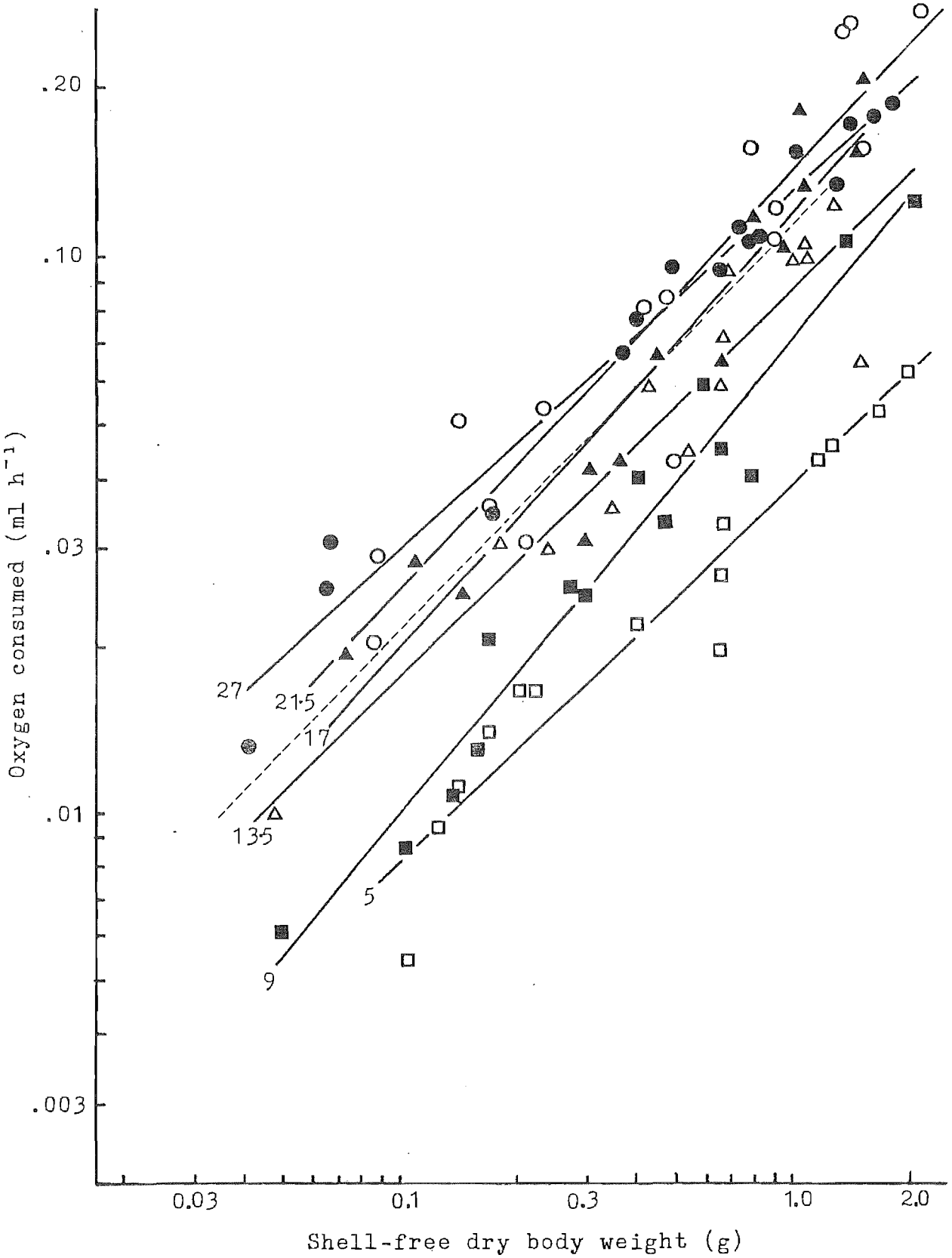


Fig. 20 - Respiration in air by high-shore chitons measured at six experimental temperatures (● 27°C, O 21.5°C, ▲ 17°C, △ 13.5°C, ■ 9°C, □ 5°C). For equations of lines, see Table 11. Broken line represents aerial respiration at 15°C reported by Murdoch and Shumway (1980).

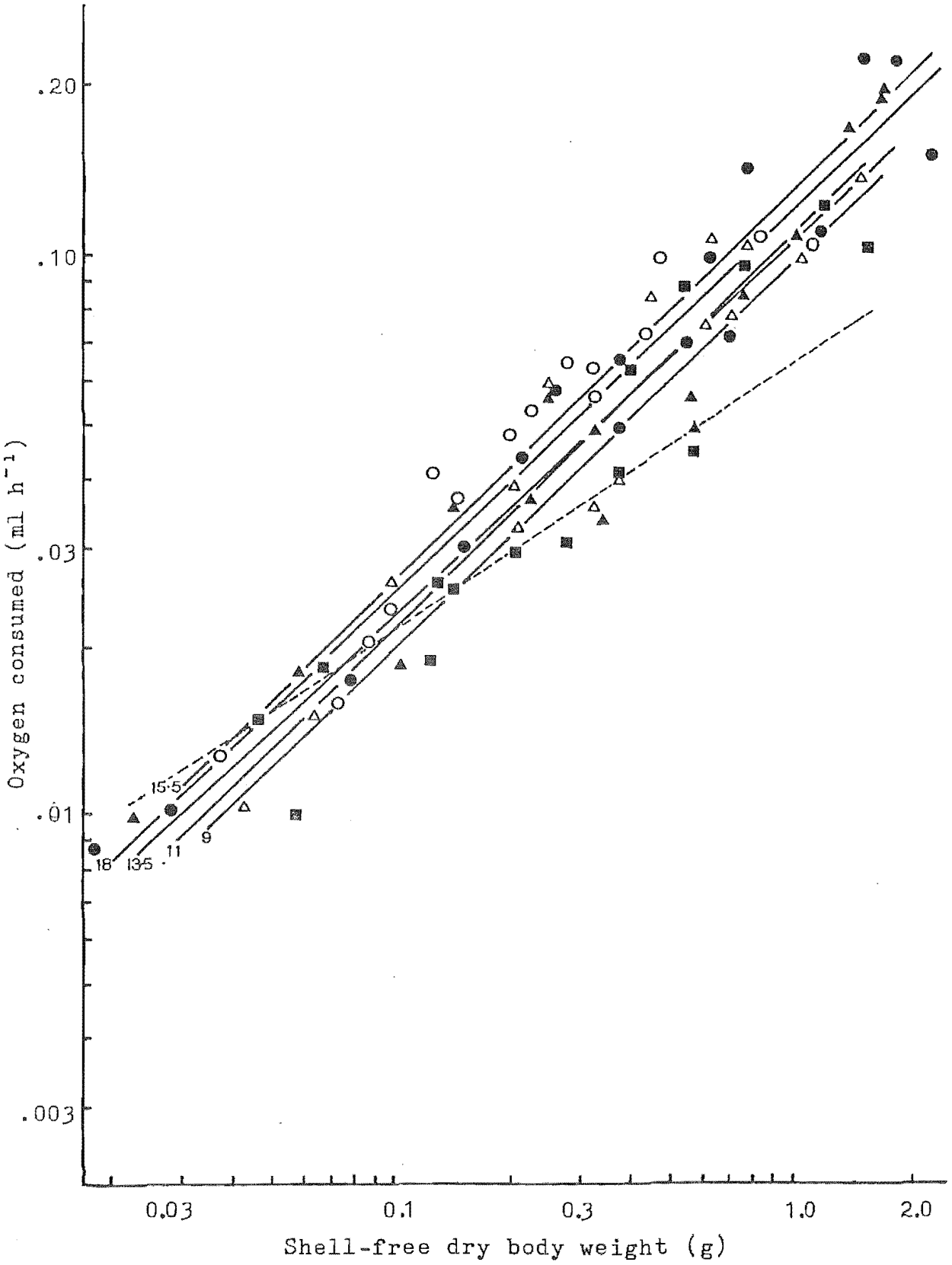


Fig. 21 - Respiration in water by high-shore chitons measured at five experimental temperatures (● 18°C, ○ 15.5°C, ▲ 13.5°C, △ 11°C, ■ 9°C). For equations of lines, see Table 11. Broken line represents aquatic respiration at 15°C reported by Murdoch and Shumway (1980).

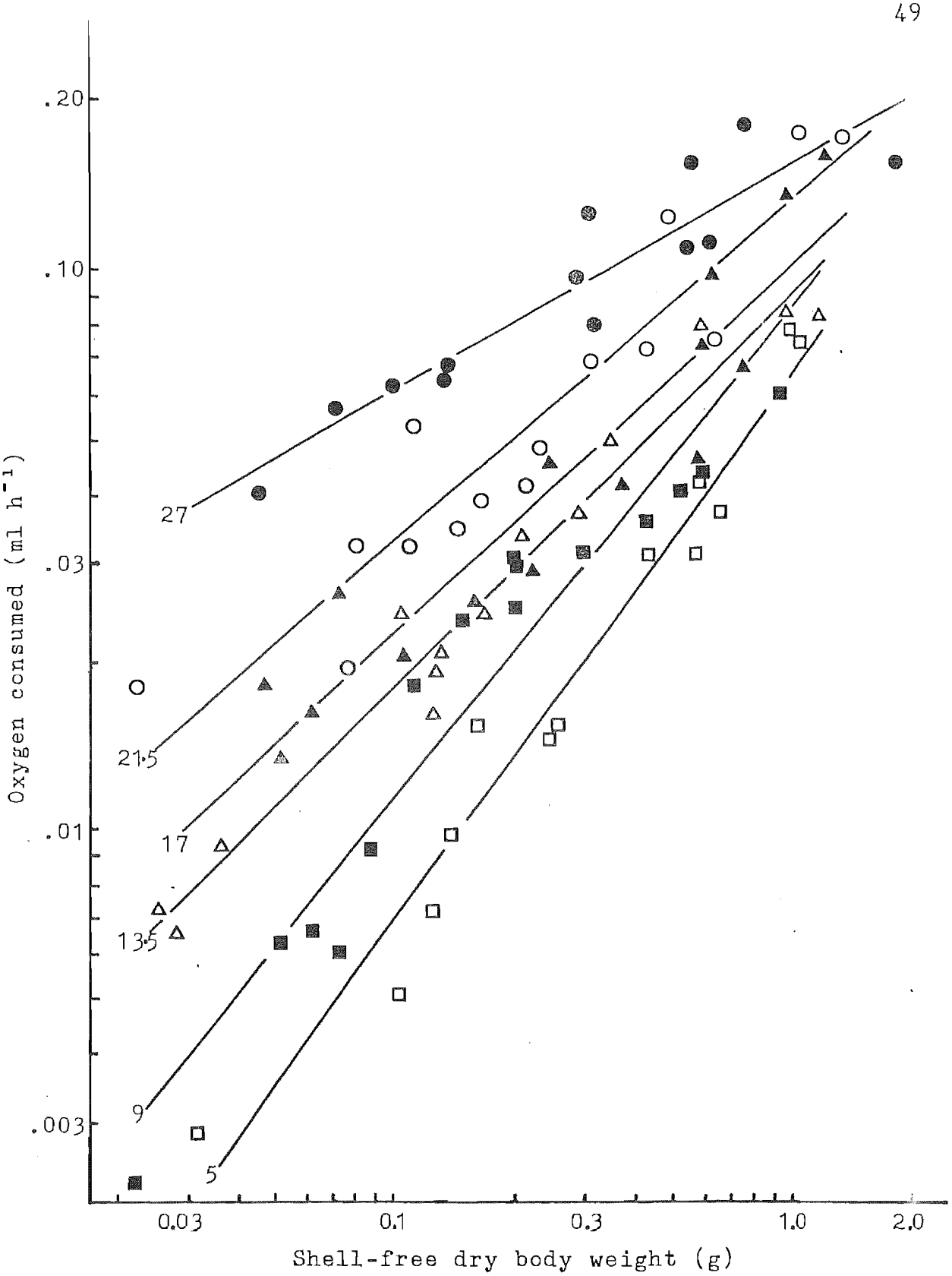


Fig. 22 - Respiration in air by low-shore chitons measured at six experimental temperatures (● 27°C, ○ 21.5°C, ▲ 17°C, △ 13.5°C, ■ 9°C, □ 5°C). For equations of lines, see Table 11.

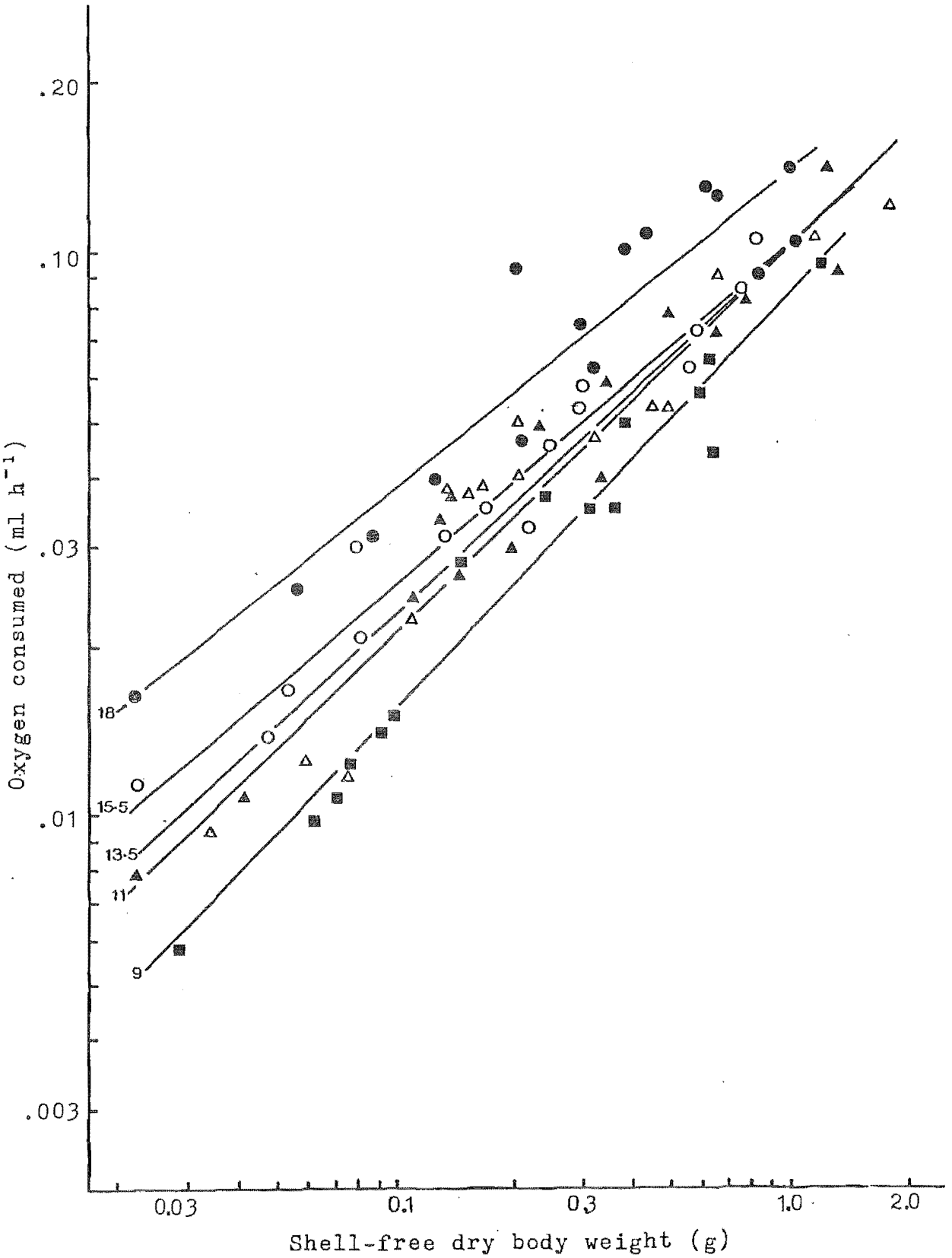


Fig. 23 - Respiration in water by low-shore chitons measured at five experimental temperatures (● 18°C, ○ 15.5°C, ▲ 13.5°C, △ 11°C, □ 9°C). For equations of lines, see Table 11.

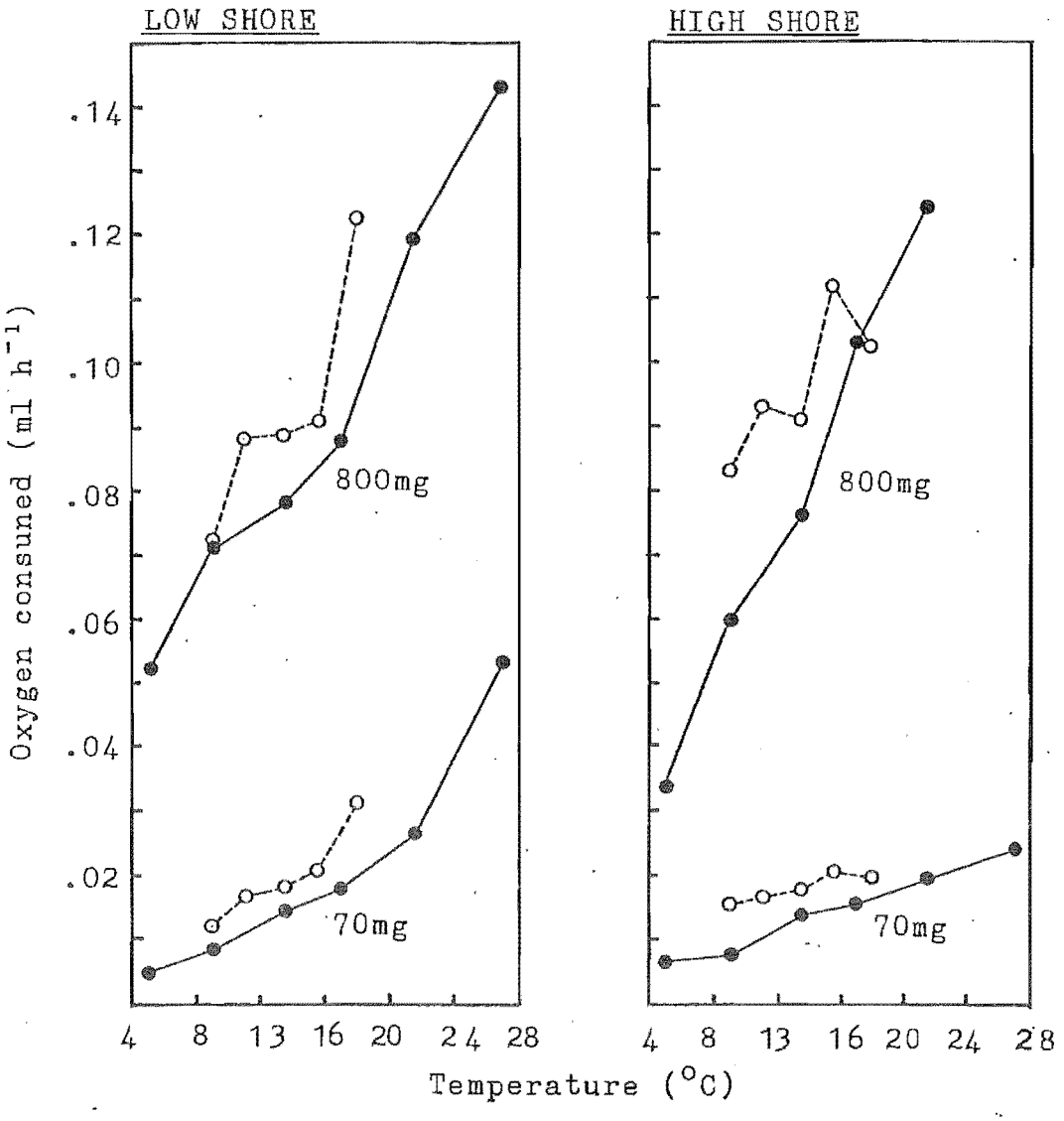


Fig. 24 - Comparison of oxygen consumption in air (——●——) and water (-----o-----) by chitons with shell-free dry body weights of 70 and 800mg.

Aquatic respiration was, on average, about 35% higher than aerial respiration at similar temperatures for animals from both groups (Fig. 24).

The dependence of respiration rate on body weight at various temperatures varied between groups as shown by changes in the weight exponent, *b* (Fig. 25). Slopes of regression lines relating *b* to temperature for high-shore aerial and aquatic respiration were not significantly different from zero (i.e., horizontal) (*F*-test, $P>0.05$) indicating that all sizes of high-shore chitons were influenced equally by temperature. However, those for low-shore aerial and aquatic respiration were significantly different (*F*-test, $P<0.01$) indicating that small chitons

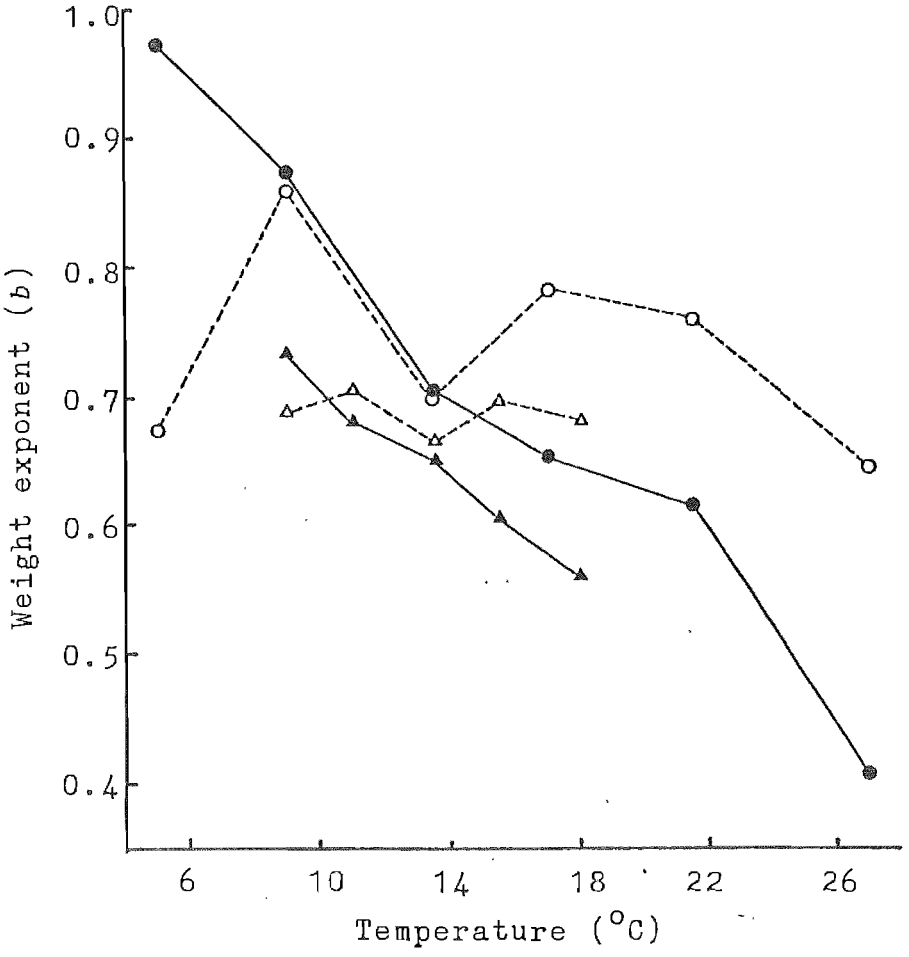


Fig. 25 - Weight exponents (b) of regression lines relating body weight and oxygen consumption at different experimental temperatures; (△ - High-shore aquatic, ▲ - Low-shore aquatic, ○ - High-shore aerial, ● - Low-shore aerial).

were affected more by increases in temperature than were large individuals.

The mean weight exponents (b values) for high-shore and low-shore chitons derived over the temperature range 9-18°C in water were 0.689 and 0.647, respectively. In air they were 0.785 and 0.745, respectively, over the range 9-17°C. Lower aquatic b values relative to those derived in air have been reported for chitons (Murdoch and Shumway, 1980) and for several *Littorina* species (Toulmond, 1967).

Temperature coefficients (Q_{10}) for oxygen consumption were calculated for standard 70 and 800mg individuals (Table 12). Respiration was more temperature dependent on the low shore than on the high shore. High-shore chitons exhibited a maximum increase in oxygen consumption of only 33% over

the complete range of environmental water temperatures to which they are exposed.

My experiments with *Sypharochiton* showed no diurnal or tidal rhythms in respiration. Regression lines relating body weight to oxygen consumption at night were not significantly different from those obtained at the same temperatures during the day (ANCOVA, $P>0.05$). No rhythmicity was apparent in aerial respiration recorded at 20 minute intervals throughout a tidal cycle.

Table 12 - Temperature coefficients (Q_{10}) for oxygen consumption. Data are expressed in terms of standard individuals of 70 and 800mg dry body weight.

	Temperature interval (°C)	High Shore 70mg	High Shore 800mg	Low Shore 70mg	Low Shore 800mg
Aerial Respiration	5-9	1.36	2.94	2.77	1.88
	9-13.5	2.94	1.61	2.49	1.21
	13.5-17	1.29	2.00	1.77	1.36
	17-21.5	1.61	1.45	2.06	1.78
	21.5-27	1.43	0.88	2.85	1.37
	$\bar{x}_{5-27}$	1.73	1.78	2.39	1.52
Aquatic Respiration	9-11	1.42	1.61	3.10	2.13
	11-13.5	1.24	0.91	1.28	1.01
	13.5-15.5	1.76	2.14	1.75	1.13
	15.5-18	0.80	0.68	3.08	2.41
	$\bar{x}_{9-18}$	1.31	1.21	2.30	1.67

The effect of activity on respiration rates of chitons is unknown. All animals were stationary during the aerial respiration experiments, whereas in the aquatic experiments there was usually an initial period of movement lasting less than 30 minutes. In a review of factors affecting respiration of intertidal invertebrates, Newell (1973) cited several studies where activity caused an increase in oxygen consumption by as much as six times the stationary rate. In many energetics studies, effects of activity have been ignored, but in others an arbitrary correction factor of x2

has been applied to respiration occurring during periods of movement (e.g., Mann, 1965; Carefoot, 1967a; Trevallion, 1971; Wright and Hartnoll, 1981). A correction factor of this magnitude appears quite acceptable in the light of experimental evidence (e.g., Newell and Roy, 1973), and thus was applied to experimental respiration for *Sypharochiton* during active periods. That is about 80% of immersion time and 33% of emersion time for low-shore chitons, and 50% and 13%, respectively, for high-shore chitons.

Total annual energy equivalents for oxygen consumption by both chiton groups are shown in Table 13.

Table 13 - Energy of metabolism (R); all units are kJ m^{-2} $year^{-1}$.

Chiton group	Aquatic respiration		Aerial respiration		Total
	Measured	Activity correction	Measured	Activity correction	
High shore	40.63	+ 20.32	37.62	+ 4.89	103.46
Low shore	144.43	+ 115.54	25.63	+ 8.46	294.06

3-4-5 Defaecation (F)

The relationship between body length and daily faecal production was best expressed as a log-log regression (as found also for herbivorous molluscs by Calow, 1975b, and Hughes, 1971a,b). The regression lines for each bi-monthly data set are plotted for the high shore in Fig. 26, and the low shore in Fig. 27. Faecal production by low-shore chitons was generally 50-100% greater than for similar sized high-shore animals at the same time of the year. The data exhibited seasonal trends which were similar for both groups. Greatest faecal production occurred in autumn (March and May), and it was least in spring (November). The defaecation rate of a chiton in May was generally about twice the rate exhibited in November.

The organic content of faeces did not appear to be related to season (Fig. 28) and the mean ash content of low-shore faeces (93.5%) was not significantly higher than that for high-shore faeces (92.8%)(t-test, $P>0.05$). However,

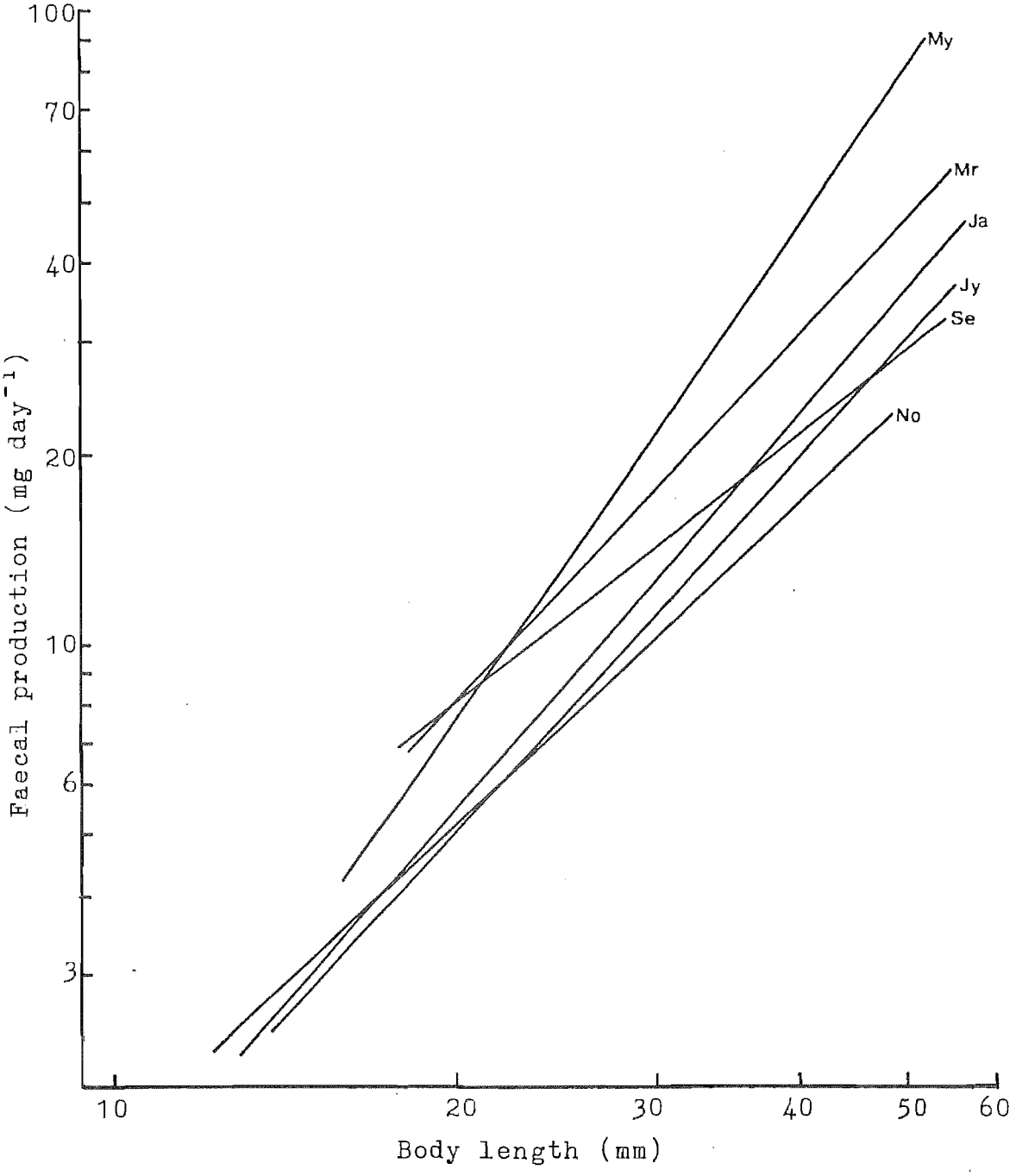


Fig. 26 - Regression lines relating chiton body length (mm) to daily faecal production (mg dry weight day^{-1}) by high-shore chitons measured six times during the year. For each line, n = 18, correlation coefficients (r) given in parentheses below. Ja = January (0.83), Mr = March (0.72), My = May (0.89), Jy = July (0.69), Se = September (0.65), No = November (0.67).

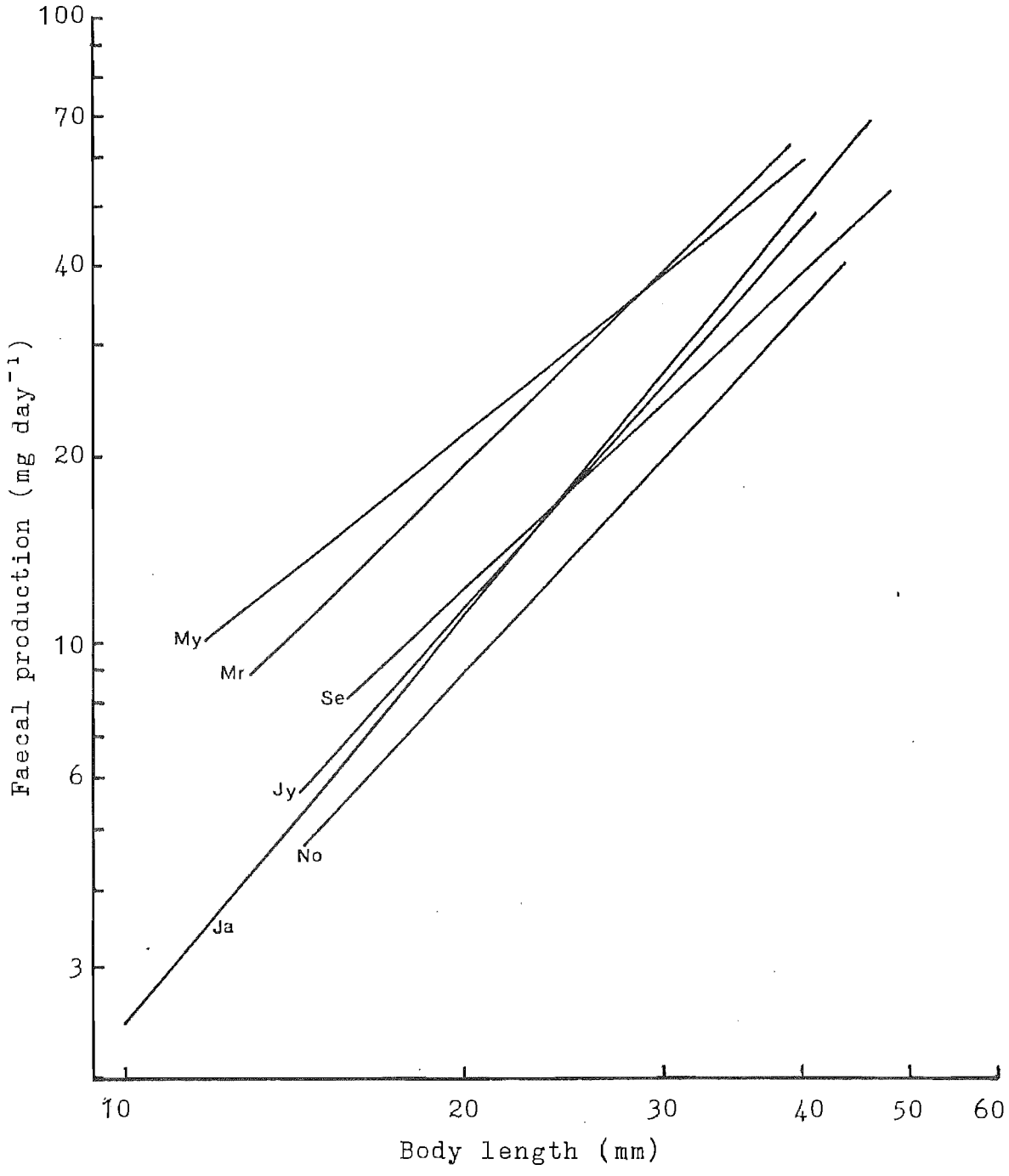


Fig. 27 - Regression lines relating chiton body length (mm) to daily faecal production (mg dry weight day^{-1}) by low-shore chitons, measured six times during the year. For each line, n = 18, correlation coefficients (r) given in parentheses below. Ja = January (0.77), Mr = March (0.82), My = May (0.84), Jy = July (0.93), Se = September (0.89), No = November (0.88).

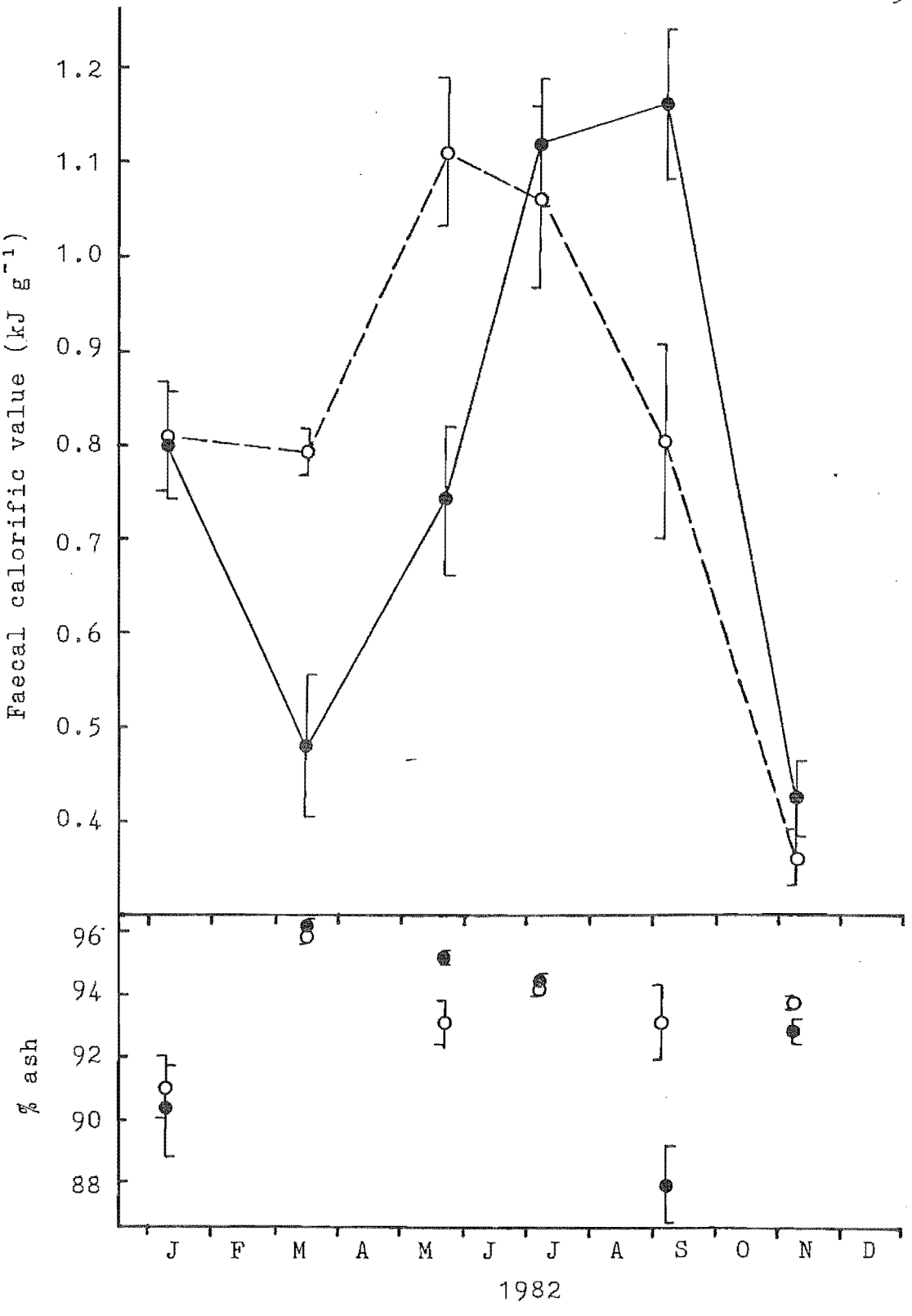


Fig. 28 - Faecal calorific content (kJ g^{-1} dry weight) ($\bar{x}$ ± S.E., n = 4) and ash content (% of dry weight) ($\bar{x}$ ± S.E., n = 3). (● - High-shore, o - Low-shore.)

energy content of faeces appeared to be strongly seasonal, although it differed between the groups (Fig. 28). Peak calorific values occurred in May-July for low-shore chitons, but in July-September on the high shore. The mean calorific value of low-shore faeces (826 J g^{-1}) was not significantly higher than the mean high-shore value (790 J g^{-1}) (*t*-test, $P>0.05$).

Annual faecal production by *Sypharochiton* on the high shore was 50.94 g m^{-2} and had an energy equivalent of 39.72 kJ m^{-2}. On the low shore, 185.45 g m^{-2} of faeces were produced; an energy value of 159.73 kJ m^{-2}. This includes mucus which constitutes a significant component of the pellets and represents a product of metabolism (Calow and Fletcher, 1972). No measurements of the mucous component of *Sypharochiton* faeces could be made, but studies of several aquatic gastropods have indicated that it can represent from 6 to 19% of the organic dry weight (Calow, 1975b; Kofoed, 1975b; Edwards and Welsh, 1982). Descriptions in Bandel (1974) suggest that gastropod faeces generally contain more mucus than those produced by chitons. Hence, mucus in *Sypharochiton* faeces was assumed to comprise 8% of the organic residue dry weight in making further calculations. Faecal production minus mucus was estimated to be 36.54 kJ m^{-2} $year^{-1}$ on the high shore, and 146.95 kJ m^{-2} $year^{-1}$ on the low shore.

3-4-6 Mucous Production (P_m)

Two mucous components were estimated; faecal mucus, and trail mucus secreted by the foot. The dry weight of faecal mucus was assumed to be 8% of the organic residue of faeces (as explained in section 3-4-5). On the high shore, this amounted to 0.29 g m^{-2} $year^{-1}$, and had an energy equivalent of 6.95 kJ. On the low shore, estimated annual faecal mucous production was 0.96 g m^{-2}, and had a calorific value of 23.01 kJ.

The dry weight of mucus secreted by the foot was linearly related to body length (Fig. 29). Annual production was estimated by taking the mean length of chitons from both groups, calculating their daily mucous production from the regression equation, multiplying those figures by the respective mean population density to give mean daily production for the groups, and finally multiplying by 365.

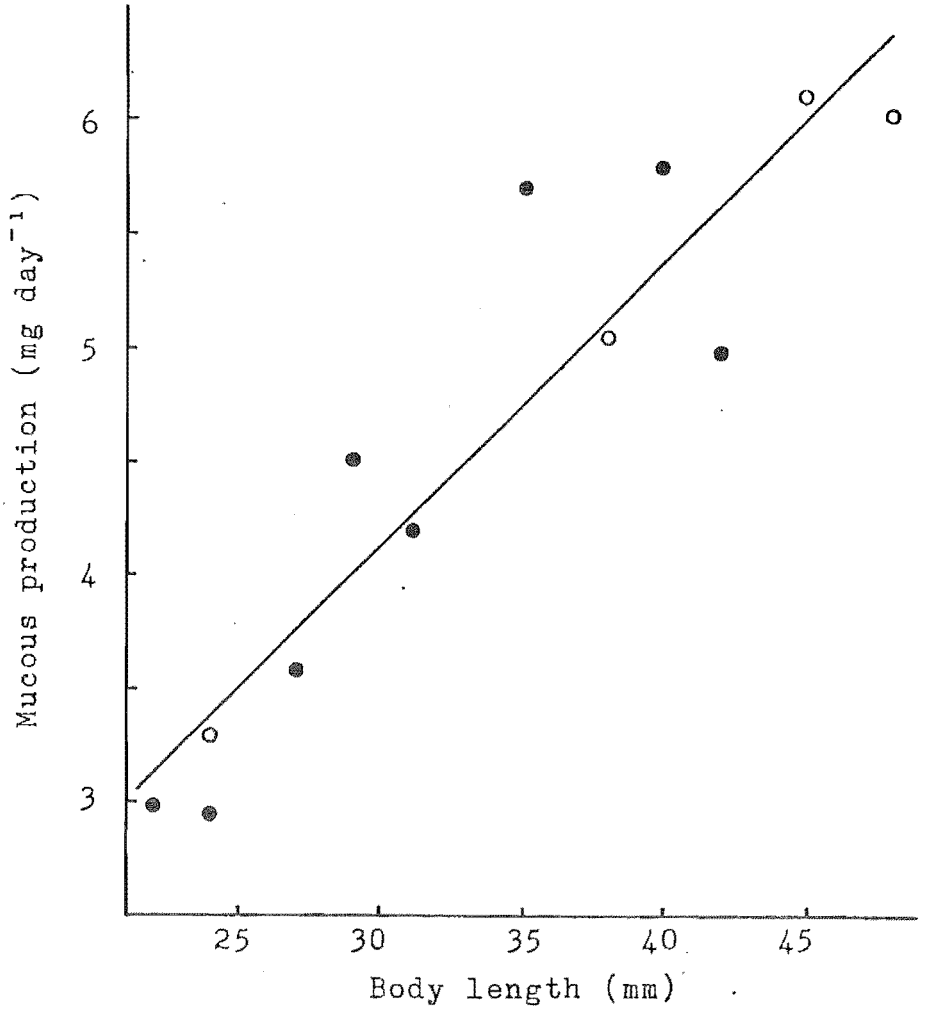


Fig. 29 - Regression line relating body length (L) to dry weight of mucus secreted daily by the foot (M). Regression equation is: $M=0.124L+0.41$, $r=0.927$. (o - High-shore chitons, ● - Low-shore chitons.)

On the high shore, 14.05 g m^{-2} of mucus with a calorific value of 336.80 kJ were produced. Low-shore chitons produced 36.06 g m^{-2} annually, the energy equivalent being 864.37 kJ.

Hence, estimated annual mucous production (the sum of faecal and foot mucus) was 343.75 kJ m^{-2} on the high shore, and 887.38 kJ m^{-2} on the low shore.

3-4-7 Excretion (U)

Quantities of ammonia nitrogen and urea nitrogen excreted by *Sypharochiton* are shown in Table 14. Ammonia nitrogen excreted per gram of chiton was greater on the low shore compared to the high shore, and the converse was true

for urea nitrogen. However, neither of these differences were statistically significant (t-test, $P>0.05$). Annual excretory losses of ammonia and urea were estimated using the mean excretion rate and mean biomass of each group. On the high shore, ammonia and urea losses amounted to 0.32 and 0.15 kJ m^{-2}, respectively, and on the low shore, 0.61 and 0.20 kJ m^{-2}, respectively. Assuming that these two components made up only 50% of the nitrogenous excretion, as suggested by Nicol's (1967) review, total excretory losses were estimated to be 0.94 kJ m^{-2} on the high shore, and 1.62 kJ m^{-2} on the low shore. It appears that excretion (U) is not a significant element of the chiton's energy budget.

Table 14 - Excretion of ammonia nitrogen and urea nitrogen (µg N excreted per gram dry weight of chiton per tidal cycle, ± S.E.). Annual mean value ($\bar{x}$ ± S.E.) obtained by combination of all individual data points. (nd = no data.)

Chiton group	Temp (°C)	Ammonia nitrogen	Urea nitrogen
High shore	9.5	6.8 ± 0.7	2.5 ± 0.7
	15.0	5.4 ± 1.5	nd
	17.0	4.2 ± 1.5	3.0 ± 0.9
	$\bar{x}$ =	5.5 ± 1.1	2.8 ± 0.8
Low shore	9.5	9.5 ± 2.0	1.3 ± 0.3
	15.0	5.7 ± 1.4	nd
	17.0	8.8 ± 2.3	3.9 ± 1.6
	$\bar{x}$ =	7.5 ± 2.1	2.6 ± 1.5

3-5 Individual Energy Budgets

Annual energy budgets for individual chitons with initial lengths (at 1 January, 1982) of 15 and 45mm, from both the high- and low-shore groups are shown in Figs 30 and 31. The only major difference between similar sized chitons from the different groups was in faecal production; low-shore chitons lost approximately twice as much energy in faeces as did high-shore animals.

Comparison of different sized animals from the same group indicated that small animals devote relatively more energy to growth production, and relatively less to reproductive production, than do large animals. Large chitons lost about twice as much energy relative to small ones via respiration, defaecation and excretion. Small chitons devote about 20% more energy to mucous production than large chitons.

It is interesting to note that the weight-specific energy requirement of *Sypharochiton* is about three times as great ($\simeq$310 J g^{-1}) for a 15mm chiton as for a 45mm animal ($\simeq$95 J g^{-1}). Similarly, the weight-specific area cleared per radular rasp is about three times as great for a 15mm, compared with a 45mm chiton (section 3-4-1).

Both consumption and respiration varied considerably throughout the year due to their dependence on temperature. A simple comparison of their relative magnitudes was made by calculating daily consumption (C_m) and respiration of 35mm chitons from both groups when the mean temperatures of air and water were about 17°C (in February) and 9°C (in August). These data indicated that metabolism accounted for a greater proportion of ingested energy in winter than in summer (Table 15).

Table 15 - The relationship between energy consumption (C_m) and respiration (R) for 35mm chitons kept at environmental temperatures of 9 and 17°C.

Chiton group		17°C (February)	9°C (August)
High shore	Cm	218 J/day	87 J/day
	R	24 J/day	16 J/day
	R:Cm	11%	18%
Low shore	Cm	294 J/day	103 J/day
	R	33 J/day	21 J/day
	R:Cm	11%	20%

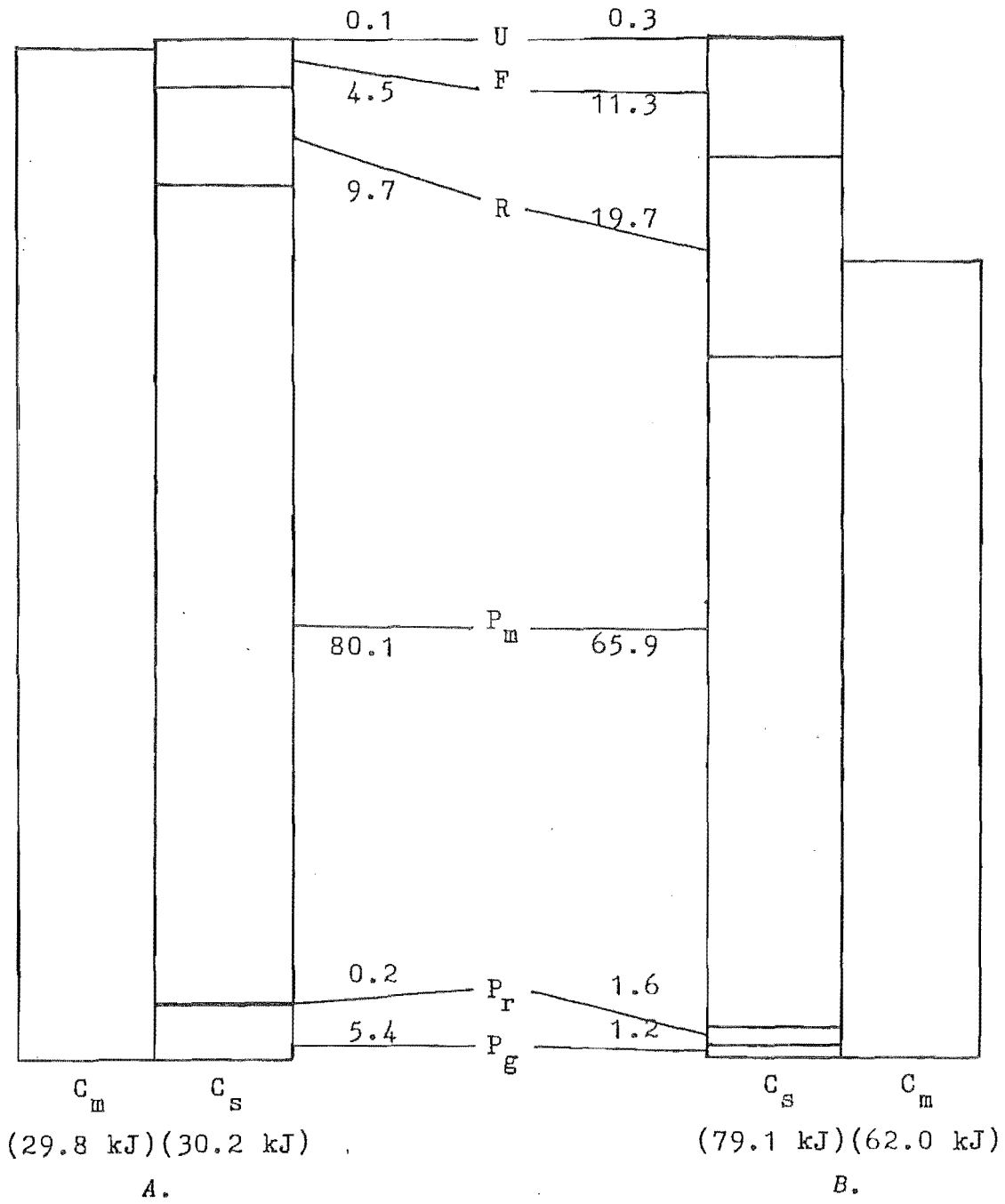


Fig. 30 - Comparison of annual energy budgets of individual high-shore chitons with initial body lengths of 15mm (*A.*) and 45mm (*B.*). Abbreviations as defined in the text. Numbers show the percentage of C_s made up by each component.

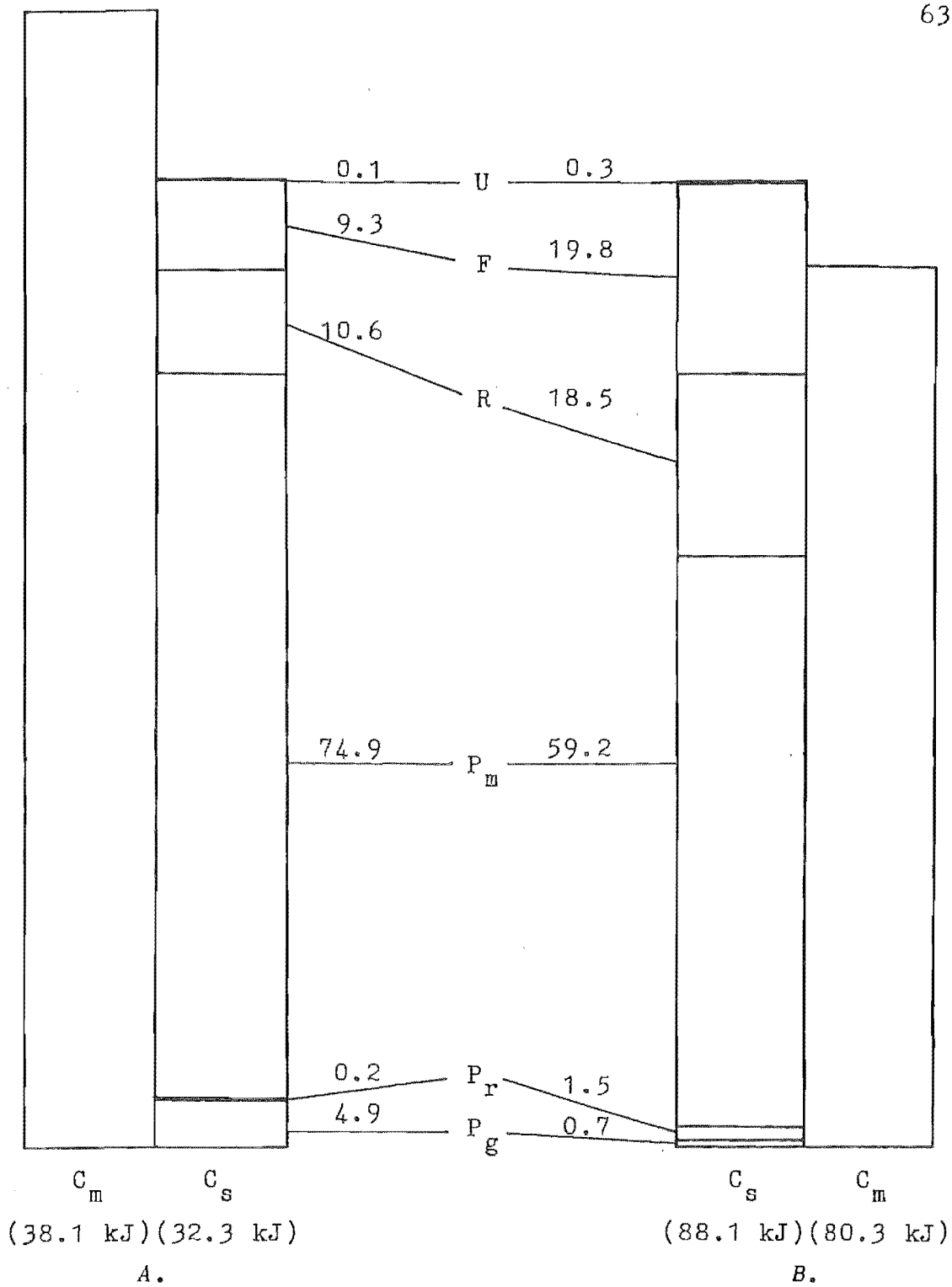


Fig. 31 - Comparison of annual energy budgets of individual low-shore chitons with initial body lengths of 15mm (*A.*) and 45mm (*B.*). Abbreviations as defined in the text. Numbers show the percentage of C_s made up by each component.

3-6 Annual Energy Budgets

The calculated values of all components of annual energy budgets (for 1982) for both high- and low-shore chiton groups are shown in Table 16. All components of the low-shore budget are higher than for the high-shore budget, generally by a factor of 2 to 3. Energy equivalents of consumption, mucous production and respiration are all about three times higher per square metre on the low, relative to the high shore. However, high-shore chitons lose relatively less energy via defaecation, and put relatively more energy into reproductive production than low-shore chitons

The flow of energy in each group is depicted in Fig. 32.

Table 16 - Components of the energy budgets for high-shore and low-shore chiton groups. (Biomass (B) in kJ m^{-2}; energy components in kJ m^{-2} $year^{-1}$.)

Chiton group	B	C_m	C_s	P_g	P_r	P_m	R	F	U
High shore	72.7	471	509	18.6	5.3	344	103	36.5	0.9
Low shore	112.7	1521	1375	36.2	8.7	887	294	147	1.6

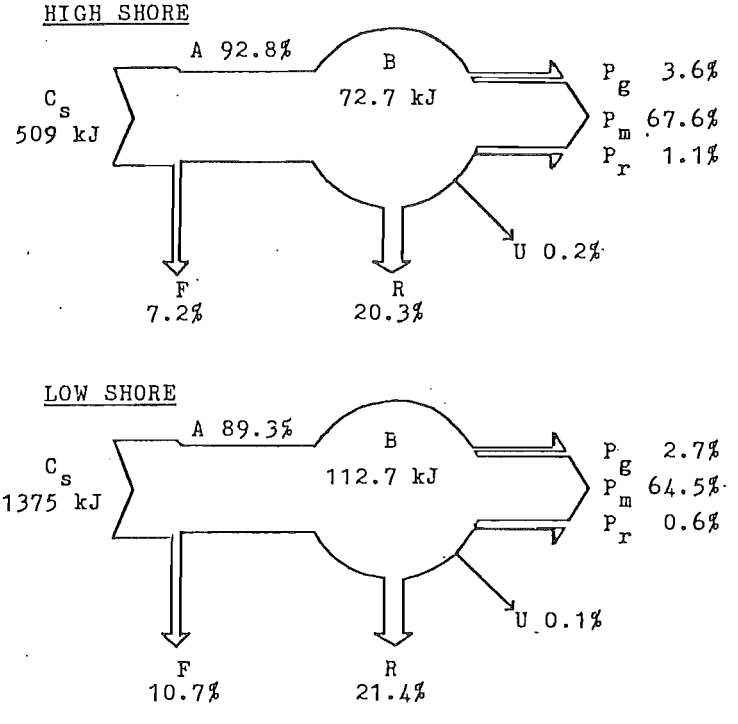


Fig. 32 - Annual energy flow per square metre for the high-shore and low-shore chiton groups. Budget components expressed as a percentage of C_s. (B = biomass, all other abbreviations as described in text.)

4. DISCUSSION

4-1 Biology of *Sypharochiton pelliserpentis*

Introduction

Several workers have examined various aspects of the biology of *Sypharochiton pelliserpentis*. Boyle (1969, 1970) studied the ecology and reaction to osmotic stress of *S. pelliserpentis* near Waitemata Harbour. The breeding biology and taxonomy of *S. pelliserpentis* were studied by Johns (1960), and I have compared physiological, structural and behavioural adaptations to environment of high- and low-shore groups of *S. pelliserpentis* in Mudstone Bay, Kaikoura (Horn, 1981, 1982). Recently, Freeth (1982) looked for differences in enzyme structure and activity between high- and low-shore *S. pelliserpentis* but found no significant variations and concluded that differences shown by the two chiton groups (Horn, 1981, 1982) were the result of phenotypic, rather than genotypic, adaptive strategies.

The following section of the discussion deals with aspects of the biology of *Sypharochiton pelliserpentis* that arose from the present study, but which are not associated primarily with the compilation of the energy budget.

Migration

Sypharochiton pelliserpentis, particularly those in their first and second years, were shown to migrate from the low to the high shore and the number migrating appeared to be inversely related to recruitment success. Migration was considerable in 1981-82, but negligible in 1982-83. Such findings suggest that migration may occur as a response to increasing density on the low shore, hence reducing competition for food. Branch (1975) considered that competition for food induced upshore migration of several *Patella* species. As the amount of organic matter available as food at both shore levels was similar, it would be expected that migration would act to minimise intraspecific competition and make consumption per unit area the same for both groups. However, as total consumption, and chiton density, were lower on the high shore, it seems likely that the high shore was the lesser preferred habitat. The high

shore is physically harsher than the low shore in terms of desiccation risk, although high-shore *S. pelliserpentis* exhibit physiological adaptations to reduce desiccation stress (Horn, 1982). Nevertheless, the probability of survival is much greater on the high than the low shore, due mainly to the greater threat of predation on the latter. I suggest that, despite reduced survival chances, the low shore is the preferred habitat of *S. pelliserpentis*, and that migration to the high shore occurs as a response to low food levels.

Johns (1960) suggested that migration by low-shore *Sypharochiton pelliserpentis* to the high shore occurred only after their valves became old and eroded, and the light-sensitive aesthetes had been worn off. However, I found eroded high-shore chitons that were still negatively phototaxic. Also, many young low-shore chitons migrate before any serious valve erosion has occurred.

Feeding Behaviour

High-shore *Sypharochiton pelliserpentis* fed only while immersed at night. Such behaviour may reduce predation risk, as a grazing chiton would be more exposed to predators on an open high-shore platform than amongst low-shore boulders, (as suggested for *Tonicella lineata* by Demopulos, 1975). Nocturnal feeding has been reported for several chitons. *Acanthozostera gemmata* and *Acanthopleura granulata* fed only at night when immersed (Thorne, 1968; Glynn, 1970), whereas *Chiton tuberculatus* fed only at night when emersed (Glynn, 1970). Feeding by *Katharina tunicata* was highly variable, and an animal might feed in extended sessions once or twice a day, or not at all for a few days (Himmelman and Carefoot, 1975). However, like low-shore *S. pelliserpentis*, intertidal *Tonicella lineata* usually grazed when immersed during both daylight and darkness, possibly to maximise respiratory efficiency and reduce desiccation stress (Demopulos, 1975). Grazing by low-shore *S. pelliserpentis* during emersion was usually carried out under the cover of dense stands of the alga *Hormosira banksii*, which would give some protection from terrestrial predators and desiccation risk.

Present data on rasping rates of *Sypharochiton pelliserpentis* confirm Kitting's (1979) observations that chitons rasp at a slower rate than other molluscs in the

same environment.

Seasonal calorific variation of tissue

Seasonal variations in the calorific content of somatic and reproductive tissue of *Sypharochiton pelliserpentis* were noted, and it was considered possible that these variations were linked. Several studies have dealt with seasonal changes in chemical composition of various body parts of North American chitons, mainly *Katharina tunicata*, but also *Mopalia hindsii* and *Cryptochiton stelleri*, and the results, which generally were consistent between studies and species, are summarised below.

Proportion of lipid increased with maturation of ovaries, but remained approximately constant throughout the year in testes (Giese and Araki, 1962; Tucker and Giese, 1962; Giese and Hart, 1967). Ovaries had a higher proportion of lipid than testes (Lawrence and Giese, 1969). Lipid was stored also in the foot, digestive gland and mantle (Giese and Araki, 1962), but Nimitz and Giese (1964) found no evidence of this lipid being used during normal gametogenesis by *Katharina*. However, starvation could cause a depletion of lipid stocks and a reduction in reproductive production (Giese and Araki, 1962; Nimitz and Giese, 1964; Lawrence and Giese, 1969), as well as a reduction in the size of the digestive gland (Lawrence *et al*, 1965). *Cryptochiton* exhibited an inverse relationship between the sizes of the gonad and digestive gland (Lawrence *et al*, 1965), and it appeared likely that the digestive gland functioned as a storage organ for lipid. The protein content of male and female gonadal tissue increased with maturation (Giese and Araki, 1962; Tucker and Giese, 1962), and although seasonal changes in somatic tissue were not apparent, blood protein was lowest when gonad index was highest (Giese *et al*, 1959). Glycogen levels in both somatic and reproductive tissue were inversely related to gonad index (Giese and Araki, 1962; Tucker and Giese, 1962; Giese and Hart, 1967). *Lepidochitona cinereus* from Scotland exhibited maximum glycogen levels after spawning, and maximum lipid content just prior to spawning (Baxter and Jones, 1978b).

Calorific values of *Sypharochiton pelliserpentis* tissue indicate some trends similar to those described above. Lipid, a major component of reproductive tissue, has a

calorific value of about 24 kJ g^{-1}, considerably more than the other components, protein (18 kJ g^{-1}) and glycogen (16 kJ g^{-1}). Hence, changes in the proportion of gonad lipid present are probably the main cause of calorific changes. The aforementioned biochemical studies suggest that the ash-free calorific content of ovaries is likely to be greater than that of testes. The calorific content per gram of testes should remain relatively constant throughout the year, whereas that for ovaries should vary, being highest during spawning and lowest during the spent phase. Such trends were exhibited by *S. pelliserpentis* gonadal tissue.

Parry (1982) found seasonal variations in the ash content of four limpet species from Australia (maximum about April and minimum about October), and he assumed that these variations were responsible for variations in the calorific value of somatic tissue, a condition which did not apply to *S. pelliserpentis* in my study. As for gonadal tissue, variations in the calorific content of somatic tissue probably were caused by changes in proportions of lipid present. Whereas changes in calorific values of high-shore somatic tissue paralleled changes in gonad indices (increasing with gonad index increases), calorific values of low-shore chiton tissues were inversely related to gonad development. These differences suggested different patterns of lipid storage and utilisation in the two groups. Three of the factors which Lawrence (1976) noted may affect the pattern of lipid storage in marine invertebrates could apply to *Sypharochiton*: the physical environment, the annual reproductive cycle, and the nutritional state of the animal.

Physical environment was unlikely to cause differences in lipid storage between groups as both groups experienced similar conditions. The reciprocal relationship between somatic calorific value and gonad index for low-shore chitons suggests that lipid is stored in the somatic tissue during the resting phase and then transferred to the gonad during gametogenesis (as demonstrated by Lawrence *et al*, 1965; Lawrence, 1976; Simpson, 1982). However, while annual reproductive requirements may explain calorific variation in low-shore chitons, this argument does not appear to be valid on the high shore. The nutritional state of high-shore chitons may influence their lipid storage patterns. Somatic calorific values decreased during the summer and early autumn,

then increased during winter and early spring. It is possible that the high-shore *Ulva* bloom which occurred during winter and early spring may have had a greater influence on consumption than was assumed, hence causing marked seasonal fluctuations in energy available to chitons. That low-shore chitons were able to build up lipid reserves during most of the year, whereas high-shore chitons could do so only during the winter *Ulva* bloom is a suggestion open to conjecture. However, it is supported by the measured annual consumption (C_m) of high-shore chitons being about 20% less than for similar sized low-shore animals.

Lower calorific values of somatic tissue of immature, relative to mature chitons suggested changes in biochemical composition occur with age. Paine (1971) found a similar reduction in calorific values for immature *Tegula funebralis* and concluded that an energetic advantage was gained by building a growing individual initially out of "cheap" material, and later adding tissues of higher value when the individual was capable of making a genetic contribution to the population.

Control of the reproductive cycle

Although only portions of two complete annual reproductive cycles of each chiton group were examined, it was clear that there was variation between cycles both in time of spawning and in amount of energy spent on reproductive production (P_r). Such variations are commonly reported for marine invertebrates and have been exhibited by several chitons (Giese, 1969; Himmelman, 1978, 1979). Both *Sypharochiton pelliserpentis* groups exhibited lower reproductive production in the 1982-83 summer than in the previous season. Factors that regulate gametogenesis in chitons usually are food availability and temperature (Pearse, 1979). However, the required stimuli can differ between species and locality, causing sympatric species, or similar species from different localities, to spawn at different times of the year (e.g., Glynn, 1970). Evidence that nutrient stores may be related to reproduction (Lawrence *et al*, 1965), and that starvation is known to reduce P_r (Nimitz and Giese, 1964) has been discussed already. However, no evidence of a food shortage in 1982 that would cause a reduction in P_r was shown by this study. Lower than average sea water temperatures were

recorded at Kaikoura during the latter half of 1982 and early 1983. If gametogenesis in *S. pelliserpentis* is governed by rising temperatures, then the lower sea temperatures could explain the P_r reduction in late 1982. However, lower temperatures could also influence gametogenesis if it is nutrient limited, as it was shown that metabolism took up a greater proportion of consumed energy at low, compared to high temperatures. This would result in less energy being available for gonad development.

Spawning by *Sypharochiton pelliserpentis* corresponded closely with the time of high spring tides, and could occur once or several times during the period from February to April (Johns, 1960). It is probable that other stimuli act in conjunction with tides to elicit spawning, and so result in differences between years. Himmelman (1981) showed that gamete release by several chiton species was correlated with phytoplankton bloom, and he argued that phytoplankton could stimulate spawning. However, slight differences in spawning times for *S. pelliserpentis* (late January to early April on the high shore, late February to late April on the low shore) suggest some other timing mechanism. Sutherland (1970) showed that the limpet *Acmaea scabra* had different reproductive patterns at different shore levels, and suggested differences in food availability as the cause. Subtidal individuals of another limpet, *Nacella macquariensis*, exhibited peak spawning two months later than intertidal individuals of the same species, suggesting that temperature increase was the primary stimulis in this case, as the water temperature peaked after the air temperature (Simpson, 1982) Neither food availability nor temperature changes seem likely to be the spawning stimuli in *S. pelliserpentis*, but as both these variables were measured rather coarsely, further experimentation is required to clarify this point.

It must be noted, however, that it was impossible to relate precisely, time and any particular stage of the gonad cycle. While spawning is probably an all-or-nothing activity at the level of the individual, it does not appear to be so for a population. At most times during the breeding cycle it was possible to find individuals with high and low gonad indices, e.g., both fully mature and recently spawned individuals were present in October when most chitons were at

the stage of mid gametogenesis. While certain stimuli may stimulate gametogenesis and spawning, it appears likely that a significant proportion of both chiton groups "ignore" the cues. Obviously, considerably more experimental information is required before the factors controlling the reproductive cycle can be determined.

Reproductive Effort

Reproductive effort, defined here as the proportion of assimilation (excluding P_m and U) that is devoted to reproductive processes (i.e., $P_r : P_g + P_r + R$), was 4.2% for the high-shore, and 2.6% for the low-shore chiton groups. Mean peak gonad indices (the mean of peak male and female indices for a group) were similar for both groups, yet high-shore chitons diverted relatively more energy into reproduction despite their lower consumption relative to low-shore animals. This does not support the theory that P_r on the high shore is limited by food availability, and indicates that high-shore chitons can make savings in other areas of their budgets that can then be spent on reproduction.

Unfortunately, no comparable figures are available for other chiton species but several intertidal gastropods have been studied in this regard. Thus, various limpet species expend between 10 and 40% of the energy equivalent of $P_g + P_r + R$ on reproduction (Sutherland, 1972; Wright and Hartnoll, 1981; Parry, 1982). On the other hand, Hughes (1971a) reported a value of 2.6% for the keyhole limpet, *Fissurella barbadensis*. Reproductive effort by various marine snails showed an even greater variation, with values between 1.2 and 3.4% for *Tegula funebralis* (Paine, 1971) and several *Nerita* species (Hughes, 1971b), 9% for *Ilyanassa obsoleta* (Edwards and Welsh, 1982), about 60% for two herbivorous *Lacuna* species (Grahame, 1982) and from 35 to 73% for the carnivore *Polinices alderi* (Ansell, 1982). It would appear, therefore, that *Sypharochiton pelliserpentis* puts a smaller proportion of its energy into reproduction than many other molluscs.

Since the maximum gonad indices for both *Sypharochiton* groups differed between seasons, so would the value of reproductive effort. Hence, a one season study does not necessarily give a typical estimate of P_r.

Variation in annual recruitment of intertidal molluscs is common (Underwood, 1979), and was exhibited by *Sypharochiton pelliserpentis*. However, recruitment success did not appear to be correlated with reproductive effort, as recruitment was about six times higher in 1981 compared with 1982, while P_r was relatively high in 1982. It is more likely that physical factors have a major influence on recruitment success, although it is also possible that the survival of recently settled larvae could be threatened by high densities of grazing molluscs (Underwood, 1979).

Mucous Production

It was unfortunate that total mucous production by *Sypharochiton pelliserpentis*, the major component of its energy budget, was so difficult to measure. Only three studies of molluscan faecal mucus have been made, and three studies of marine mollusc trail mucus are known to me. Daily trail mucous production by three low-shore limpet species (calculated from Branch and Marsh, 1978) correlated well with values obtained for *S. pelliserpentis*. The paua, *Haliotis iris*, with a shell length of 120mm produces about 12mg of mucus per day (calculated from Bloomberg, 1981), a value comparable to what was obtained by substituting the length 120mm into the regression equation relating chiton body length and mucous production. Similarly, a mud snail with a dry tissue weight of 43mg produced about 1.8mg of mucus per day (calculated from Edwards and Welsh, 1982), a figure comparable with the value of 2.3mg produced by a 43mg *S. pelliserpentis*. These three studies support the levels of mucous production calculated for *S. pelliserpentis*, and highlight the importance of mucus to crawling molluscs.

Very little attention has been paid to the histology of the chiton foot (review in Hyman, 1967). It appears that the density of mucous cells varies considerably between species, but several species tend to have a concentration of such cells along the anterior and lateral margins of the foot, and in the pallial groove between the gills and the foot. *Katharina tunicata* has numerous mucous cells covering the foot, pallial groove and mantle. Two types of mucous cell were present, each producing a different mucus (Nimitz and Giese, 1964). *Sypharochiton pelliserpentis* has a high

density of mucous cells, particularly along the foot margins (P.M. Johns, pers. comm.).

Respiration

The higher aquatic, compared with aerial respiration for *Sypharochiton pelliserpentis* is consistent with results obtained for other chitons including *Cryptochiton stelleri* (Petersen and Johansen, 1973), subtidal *Tonicella lineata* and high-shore *Nuttallina californica* (Robbins, 1975). However, Murdoch and Shumway (1980), who examined respiration in six chiton species, found that high-shore *S. pelliserpentis* had higher oxygen uptake rates in air than in water. The same authors concluded that chiton species occurring high on the shore have lower oxygen uptake rates in water than those on the low shore, but that aerial uptake was not correlated with shore height. High-shore *S. pelliserpentis* do not exhibit greater oxygen uptake in air than in water in my study. Murdoch and Shumway's (1980) relationship between oxygen consumption and body weight for high-shore *S. pelliserpentis* in air at 15°C compared well with the equation I obtained at 17°C. However, the slope of their 15°C aquatic respiration line (0.470) was considerably less than the slope I obtained at 15.5°C (0.679), indicating that larger chitons in Mudstone Bay respired in water at a relatively greater rate than those obtained from a sheltered shore in Otago Harbour by Murdoch and Shumway.

Contrary to results I obtained for low-shore *Sypharochiton pelliserpentis*, studies of gastropod respiration generally have shown no change in weight exponents (b) with change in temperature (e.g., Davies, 1966; Branch and Newell, 1978; Houlihan and Innes, 1982), although there are some exceptions (Newell and Roy, 1973; Bloomberg, 1981). The only available study of chitons giving data comparable with mine indicated no significant variation in b for aquatic respiration over a 20°C range by *Tonicella lineata* from both subtidal and low intertidal populations (Kincannon, 1975).

Excretion

Not all components of excretion by *Sypharochiton pelliserpentis* were measured, and studies of the components of excretion by other molluscs are rare. Nicol (1967)

cited analyses of nitrogenous excretion by six species (two gastropods, two bivalves and two chephalopods) and suggested that molluscs were primarily ammonotelic. Thus, ammonia comprised about 45% of the excreted nitrogen, urea amino acids and purines each comprised about 10%, and other unidentified compounds made up the remaining 25%. Only small traces of uric acid were reported. However, results of a study of five species of *Acmaea* (limpets) were very different with 40% of excretion being uric acid, 27% ammonia and 19% urea (Baribault, 1968). No studies of chiton excretion are known to me, although Myers (1920, cited in Hyman, 1967) reported the presence of urea, ammonia nitrogen, non-protein nitrogen and creatinine in the blood of *Cryptochiton*, but uric acid has not been reported from chitons. Thus it appears likely that chitons are ammonotelic and, therefore, that the ammonia and urea measured in this study comprise the major components of nitrogenous excretion.

Excretion by *Sypharochiton pelliserpentis* did not appear to be related to temperature. Whereas a positive correlation between excretion rate and metabolic rate (and hence, environmental temperature) might be expected (e.g., Wright and Hartnoll, 1981), studies of molluscs showing independence between excretion rate and temperature are available (e.g., Mace and Ansell, 1982). Rates of ammonia and urea excretion by *S. pelliserpentis* were comparable with those reported for other molluscs (review in Pandian, 1975). Therefore, I conclude that excretion was a negligible component of the energy budget, a conclusion consistent with that found for other molluscan energy studies.

Bioerosion

The high proportion of magnetite in the radular teeth of chitons (Carefoot, 1965) has led several workers to postulate that these animals can contribute significantly to substrate erosion (North, 1954; Healy, 1968; Taylor and Way, 1976). By using the non-organic fraction of faeces (47.3 and 173.4 g m^{-2} $year^{-1}$ for high- and low-shore chitons, respectively), and the mean weight of mudstone rock from Mudstone Bay (2.40 g cm^{-3}, s=0.04, n=5), erosion rates attributable to the chiton groups were calculated as 0.020 mm $year^{-1}$ on the high shore and 0.072 mm $year^{-1}$ on the low

shore. Kirk (1977) found that total erosion of the South Bay mudstone was occurring at annual rates of about 1.31mm on the low shore and 1.15mm on the mid to high shore, hence, radular rasping by *Sypharochiton pelliserpentis* caused respectively 1.7% and 5.5% of that erosion. These figures are comparable with those given for the chiton *Acanthopleura brevispinosa*, which were 0.017- 0.038 mm $year^{-1}$ or 1.7-7.6% of the total measured erosion (Taylor and Way, 1976).

4-2 Energy Budget of *Sypharochiton pelliserpentis*

Accuracy of the budget

Estimates of some components of the energy budgets for *Sypharochiton pelliserpentis* are more reliable than others. Biomass (B), growth production (P_g) and reproductive production (P_r) were based on reliable data and involved no major assumptions. Mucous production (P_m), the largest component, was based on a relatively small, although well correlated number of sample points. However, the estimate of P_m involved two major assumptions: that mucous production was constant whether the chiton was moving or stationary, and that half the produced mucus adhered to the experimental animal when it was removed from the glass slide. Edwards and Welsh (1982) assumed that stationary *Ilyanassa obsoleta* produced negligible quantities of mucus, yet Branch and Marsh (1978) showed that six *Patella* species all produced foot mucus while stationary. Respiration (R) was based on a comprehensive set of oxygen consumption curves, but the correction for activity (x2) was untested. Defaecation (F) was based on comprehensive data, although the assumption that mucus comprised 8% of the organic portion was not tested, and the possibility of dissolved organic matter leaching out of the faeces was not investigated. Edwards and Welsh (1982) found that for *I. obsoleta*, only 4% of faecal energy was readily leached; a similar proportion would be a negligible component of *S. pelliserpentis* energy budgets. Exudates (U) were slight, and even if the energy of the excreted ammonia and urea had been multiplied by a factor of eight (instead of by two, as was done), U would still have been a negligible component.

Measured consumption (C_m) was probably the least

reliably calculated aspect of the budget as it was based on four major variables (radular rasping rate, area cleared per radular rasp, time spent feeding, and the assumed calorific content of the food available), each of which depended on other variables and assumptions. However, the comparison of measured consumption with summed consumption (C_s=P+R+F+U) provides an internal check on consumption. For high-shore *Sypharochiton pelliserpentis*, C_s was larger than C_m by 8%, but for the low-shore group C_s was 9.6% smaller. Other molluscan energy budgets which have provided such a check are rare. Hughes (1970) found that C_m was 14% smaller than C_s in his study of the deposit-feeding bivalve *Scrobicularia plana*. Paine (1965), in a short-term laboratory study of the carnivorous opisthobranch *Navanax inermis*, found C_s was smaller than C_m by 8%, and Wright and Hartnoll (1981) studied a population of the limpet *Patella vulgata* for two years and found that C_s was the smaller by 15%. Considering the various extrapolations and assumptions involved in compiling these annual field budgets for *S. pelliserpentis*, discrepencies of 8% and 9.6% do not seem unreasonable, and suggest that no great error was involved in the estimation of their larger, yet less reliable, components (i.e., C_m, R and P_m).

Comparison with other budgets

Energy budget components calculated for other herbivorous intertidal molluscs are summarised in Table 17. Four points, however, should be noted before making the comparison with *Sypharochiton pelliserpentis* budgets. First, individuals of *Ilyanassa* and *Littorina* are relatively short-lived compared with *Sypharochiton*, and *Nerita* and *Fissurella* are tropical species. Differences in latitude and lifespan can influence the amount of energy spent on metabolism, growth and reproduction (Newell, 1973; Branch, 1981). Only *Patella* and *Tegula* are long-lived temperate species like *Sypharochiton*. Second, *Ilyanassa* is primarily a deposit-feeder, and although it does consume the green alga *Ulva* when it blooms during summer, its diet would be vastly different than that of *Sypharochiton*. Third, exudates (U) in the *Sypharochiton* budgets are assumed to have been derived from assimilated material (following Kofoed, 1975b),

Table 17 - Components of energy budgets for herbivorous intertidal molluscs. All values in kcal m^{-2} $year^{-1}$, except for *Sypharochiton pelliserpentis* where values in italics represent kJ m^{-2} $year^{-1}$. (*a*=assumed value, *n*=component not measured, #=herbivore and deposit feeder, $P^* = P_g + P_r$.)

Species	Location	C	A	P_g	P_r	P_m	R	A:C	P:C	P:A	R:A	P*/B	Source
Sypharochiton pelliserpentis	Kaikoura, high-shore	122 *509*	113 *472*	4.4 *18.6*	1.3 *5.3*	82 *344*	25 *103*	93	72	78	22	0.33	This study.
Sypharochiton pelliserpentis	Kaikoura, low-shore	328 *1375*	293 *1228*	8.7 *36.2*	2.1 *8.7*	212 *887*	70 *294*	89	68	76	24	0.43	This study
Ilyanassa obsoleta#	Connecticut	10616	4049	34	65	3251	637	38	32	83	16	0.63	Edwards & Welsh, 1982
Patella vulgata	Isle of Man	383	172	16.3	23	14[a]	119	45	14	31	69	0.47	Wright&Hartnoll,1981
Fissurella barbadensis	Barbados	566	190	46	5.3	*n*	139	34	9	27	73	4.1	Hughes, 1971a
Littorina irrorata	Georgia	-	290	-	-	-	-	45	6.3	14	86	0.81	Odum & Smalley, 1959
Nerita peloronta	Barbados	95	39	6.8	0.7	*n*	31	41	7.9	19	81	1.25	Hughes, 1971b
Nerita peloronta	Barbados	265	115	11.3	3	*n*	101	43	5.4	12	88	-	Hughes, 1971b
Nerita tessellata	Barbados	614	247	21	9	*n*	217	40	4.8	12	88	0.78	Hughes, 1971b
Nerita versicolor	Barbados	151	59	6.7	0.9	*n*	51	39	5.0	13	87	0.63	Hughes, 1971b
Tegula funebralis	Washington	1071	756	95	8	75[a]	578	70	16	23	77	1.40	Paine, 1971

whereas in the other studies shown (with the exception of Edwards and Welsh, 1982) U has been classified as unassimilated material. Fourth, mucous production has been measured only in this study and that on *Ilyanassa obsoleta*. The addition of mucous production (P_m) to total production (P) and assimilation (A) results in the calculation of markedly different efficiencies than those obtained when it is ignored. The effect of this last point is made clear in Table 17 by comparing the efficiencies involving P and A with those for other species.

The assimilation efficiency (A:C) and ecological efficiency (P:C) for both *Sypharochiton pelliserpentis* groups are higher than for other species. However, the A:C and P:C efficiencies can vary between species because of differences in the proportion of consumption egested. Egestion is influenced by various factors, e.g., changes in food abundance and time spent feeding (Branch, 1981), food type (Carefoot, 1970; Kofoed, 1975a), degree of starvation of the animal (Calow, 1975a), and feeding method (Odum and Smalley, 1959). It appears that the *S. pelliserpentis* groups, with A:C efficiencies of 89 and 93%, can assimilate their diatom intake relatively more efficiently than other molluscs (e.g., those cited in Table 17, and Kofoed, 1975a; Møhlenberg and Kiørboe, 1981), and may also minimise energy losses (e.g., via defaecation) because the abundance of their exploited food is not great (Branch, 1981).

The finding that respiration accounts for less than a quarter of assimilated energy, and that production (almost exclusively mucus) is the major component of assimilation, is contrary to the commonly held view that respiration accounts for the bulk of assimilated energy in animal energy budgets (Table 17) (McNeill and Lawton, 1970; Branch, 1981). In several energy budgets for marine invertebrates in which ingestion and defaecation were measured directly, the sum of tissue production and respiration was less than the total assimilation (calculated by difference). Many of these budgets were for sea urchins (review in Miller and Mann, 1973; Greenwood, 1980) and indicated that between 30 and 90% of assimilated energy was unaccounted for. However, some were for molluscs including Leighton's (1968, cited in Miller and Mann, 1973) budget for *Haliotis rufescens* in which about 68% of the energy assimilated was not accounted for. In studies

of three opisthobranchs, Carefoot (1967a,b) found that production and respiration accounted for only 60% of absorbed energy, although he balanced his budget by doubling respiration and assuming that the remaining 15% of absorbed energy was lost via excretion and mucous secretion. Edwards (1979, cited in Edwards and Welsh, 1982) also showed that the sum of tissue production plus respiration by the mud snail *Ilyanassa obsoleta* fell short of total assimilation by up to 78%. Two studies of carnivorous gastropods found that respiration accounted for only 11 to 30% of ingested energy (Ansell, 1982; Berry, 1983). These studies of echinoderms and molluscs indicated clearly that a significant component of energy loss was not being measured.

Dissolved Organic Matter and Mucus

Miller and Mann (1973) suggested that dissolved organic matter (DOM), a previously unmeasured component of energy budgets, could account for the unexplained energy shortfalls outlined in the previous section. Various studies concerning annelids, crustaceans and echinoderms supported their hypothesis (Johannes and Satomi, 1967; Hargrave, 1971; Field, 1972; Jørgensen, 1976), however, no evidence has been published suggesting that DOM fluxes play an important role in molluscan energetics.

The energy shortfall for *Ilyanassa obsoleta* was accounted for completely by mucous production (comprising 80% of assimilated energy), and DOM releases represented less than 1% of assimilated energy (Edwards and Welsh, 1982). Such a P_m:A ratio supports those obtained for both groups of *Sypharochiton pelliserpentis* (72 and 73%). Calow (1974) found that mucous secretion by two fresh water pulmonates accounted for 13 to 22% of assimilated energy. Calow suggested that mucous production during locomotion was more important to members of the Pulmonata than other mollusc groups as pulmonate locomotion depends on cilia which require a mucous trail for leverage. Branch (1981) estimated the contribution of mucus to the energy budget of the limpet *Patella longicosta*, using the mucous secretion rate of a stationary limpet (Branch and Marsh, 1978), to be almost half the production, or about 10% of assimilation. The inability to obtain measurable amounts of mucus from the

trails of moving *Patella* spp. led Branch (1981) to conclude that little energy was spent on mucous secretion during locomotion. Similar technical problems were encountered in my study. However, this was not surprising, since if chitons produce mucus at a rate similar to that of the mud snail *I. obsoleta*, then a 35mm chiton would have to travel almost 0.5m to deposit 1mg of mucus. I concluded that mucous production was slight but continuous, and hence, dependent more on time than on activity.

Although uncertainty surrounds the actual advantages imparted by mucous secretion, it is clear that mucus must have an important survival value for *Sypharochiton pelliserpentis* since it is such a major component of the budget. Mucus can have other functions besides being a medium for more efficient locomotion, however. It is used to bind faecal pellets, thereby reducing the risk of egested material fouling the gills or mouth (Calow, 1974). It is essential for adhesion (Grenon and Walker, 1981), and for this reason will be important for stationary, high-shore chitons which experience long periods of emersion. It is also likely to be important as a means of keeping the gills moist during exposure to air (Robbins, 1975), and mucocytes in some limpets appear to have an offensive function (Branch and Branch, 1980), although this has not been shown for chitons. Further, mucus may have an enriching effect on the environment by becoming a medium for bacterial growth. Calow (1974) found that the mucous trails of *Planorbis contortus* soon became colonised by bacteria which were the preferred food of *P. contortus*, and that the bacteria had a higher ash-free calorific value than available periphytic diatoms. Such enrichment could also benefit chitons grazing on microscopic organic films. It is likely, therefore, that the relatively high mucous production by chitons is not solely an aid to locomotion. In retrospect, this component should have been more exhaustively examined, particularly to test for differences in secretion rate between moving and stationary, and immersed and exposed animals. Any future energetics studies of molluscs must consider this component seriously.

Production to Biomass (P/B) Ratio

The P/B ratio is a measure of metabolic activity, and is negatively correlated with longevity, indicating that high turnover rates are linked with low longevity (Robertson, 1979; Branch, 1981). The P/B ratios (where $P=P_r+P_g$) of the high- and low-shore *Sypharochiton pelliserpentis* groups (0.33 and 0.43, respectively) were lower than those cited by Robertson (1979), but fit well on his regression line correlating P/B ratios with longevities (assuming longevities of 23 and 18 years for high- and low-shore groups, respectively). Thus, it appears that *S. pelliserpentis* have adopted a strategy of extremely low production relative to other molluscs. The negative relationship between P/B ratios and longevities appears to be generally applicable to many marine macrobenthic species, and such a relationship can be used to provide an estimate of one variable, given the other (Robertson, 1979).

Food energy available on the substratum

To my knowledge, the method outlined here to estimate organic energy available on the substratum has not been used before. Typically, total microalgal biomass is estimated based on chlorophyll *a* present on the rock surface (e.g., Gifford and Odum, 1961; Nicotri, 1977). This estimate of food, however, is very variable due to the presence of other plant pigments (Nicotri, 1977) and the fact that detritus is not fully represented due to pigment degradation in dead plant matter.

However, Nicotri's (1977) data from uncaged, grazed areas of rock do provide some comparison with my results of total organic matter available on the rock surface. Nicotri showed that seasonal fluctuations in levels of chlorophyll *a* occurred, particularly on the high shore, and that the actual annual amplitude varied considerably, being 5mg m^{-2} in 1971-72 and only 0.5mg m^{-2} in 1972-73 in the high intertidal. Over a three year period on a sheltered shore, the quantity of chlorophyll *a* was slightly higher on the low shore, being between 0.75-6.0 mg m^{-2}, compared with 0.4-5.5 mg m^{-2} in the high intertidal. Nicotri's (1977) results are comparable with my findings of the weight of organic matter available per unit area in Mudstone Bay; approximately equal quantities at both shore levels, no clear seasonal trends, and differences

in maximum and minimum values being less than a factor of three.

Consumption

Dependence of radular rasping rate on temperature and body size, as shown for *Sypharochiton pelliserpentis*, has been demonstrated for several molluscs. For example, the gastropods *Littorina littorea* (Newell *et al*, 1971), *Cellana ornata* (Boyden and Zeldis, 1979) and *Melagraphia aethiops* (Zeldis and Boyden, 1979) have rasping rates positively correlated with temperature. Size dependence has been demonstrated for *Littorina littorea* (Newell *et al*, 1971) and for *Melagraphia aethiops* at 15°C, but not at 9 or 10°C (Zeldis and Boyden, 1979).

The lower weight-specific consumption of high-shore chitons relative to the low-shore group clearly indicates that they are energetically disadvantaged compared to low-shore chitons. However, high-shore chitons exhibit various adaptations to make up this shortfall or to conserve energy. These will be discussed now.

Whereas low-shore chitons can feed at virtually any time of day and any stage of the tide, high-shore chitons feed only at night while immersed. Therefore, to achieve parity of consumption, high-shore chitons would have to feed faster, or more consistently, or on a food with a higher energy content per "bite". No differences were apparent in food quality at the different sites and neither was there any difference between radular rasping rates at different shore levels. This similarity of high- and low-shore rasping rates is in contrast to results obtained by Zeldis and Boyden (1979) showing that high-shore *Melagraphia aethiops* compensated slightly for a reduction in available feeding time by increasing their rasping rate. Similarly, Newell *et al* (1971) considered that *Littorina littorea* exhibited rasping rate differences that compensated almost exactly for shore level differences in feeding time; however, Cornelius (1972) could identify no compensatory response in *L. littorea*.

Instead of increasing their rasping rate, it appears that high-shore *Sypharochiton pelliserpentis* spend more than twice as much of their movement time feeding compared with low-shore chitons. My observations showed that high-shore

chitons commensed feeding soon after immersion and fed fairly consistently throughout the immersion period, a trend exhibited by other high-shore molluscs (Newell *et al*, 1971; Boyden and Zeldis, 1979; Zeldis and Boyden, 1979). In contrast low-shore chitons fed discontinuously, and spent a large proportion of their movement time not feeding. Although no measurements of crawling rates were made in this study, Beckett (1969) found that *S. pelliserpentis* crawled faster on the high compared with the low shore. Shore level similarly influenced the behaviour of *Melagraphia aethiops* (Zeldis and Boyden, 1979), and two *Cellana* limpet species (Beckett, 1969). A faster crawling rate while feeding would cause a smaller overlap of consecutive rasped areas, and hence,potentially a greater energy intake per rasp. The mean overlap of consecutive rasps recorded on the perspex plates of cultured microalgae was 30%, but if it were reduced to 20% then the chiton would increase its energy consumption by about 14%. An increase in crawling speed would have the negative effect of increasing metabolic demands, but I suspect an animal would be unlikely to maintain such behaviour if the disadvantages outweighed the gains.

Despite the compensations made, and excluding any correction due to crawling rate, high-shore chitons still consumed about 20% less energy than low-shore animals. (Zeldis and Boyden, 1979, calculated a similar discrepency of 18% between high- and low-shore *Melagraphia aethiops*.) Therefore, it would appear that high-shore *Sypharochiton pelliserpentis* partition their consumed energy differently from individuals on the low shore.

On a weight-specific basis, small chitons consumed more food than large animals. Similar findings have been shown for *Pila globosa* (Haniffa and Pandian, 1974) and *Melagraphia aethiops* (Zeldis and Boyden, 1979). Such weight-specific consumption is in agreement with currently accepted total metabolism - body weight relationships (Zeuthen, 1953; Hemmingsen, 1960), and is supported by the calculated individual energy budgets which showed that smaller chitons required relatively more food.

Adaptations in metabolic energy expenditure

A reduction in energy losses via metabolism can be

achieved by various physiological and behavioural adaptations including reduced level of metabolism, reduced temperature dependence of metabolism, acclimation, differential respiration in air and water, reduced activity on a seasonal or short-term basis, and rhythmic regulation of metabolism (Branch *et al*, 1979). In this study, acclimation was not examined and no daily respiratory rhythms were observed.

High-shore chitons exhibited reduced temperature dependence of metabolism, particularly for aquatic respiration, compared with low-shore chitons. This reduced dependence can be related to the need to minimise metabolic costs at high temperatures which are usually experienced during daytime low tides at high shore. Low-shore chitons were likely to be exposed to high air temperatures for up to two hours each day, compared with a possible 12 hours on the high shore. It was noted that the Q_{10} values for low-shore chitons were smallest in the middle of the experimental temperature range, particularly for aquatic respiration. Davies (1966) showed a similar trend with Q_{10} values for *Patella vulgata* and suggested that this was a form of acclimation which kept metabolism relatively constant over the most frequently experienced environmental temperature range. Intraspecific differences in metabolic rate related to shore level have been shown for several limpet species (e.g., Davies, 1966, 1967; Smith, 1975). However, *Sypharochiton pelliserpentis* did not exhibit comparable trends of lower metabolic rates for high-shore individuals. Oxygen consumption curves calculated in the mid range of environmental air and water temperatures were virtually identical for both shore levels. The dependence on temperature of the slope (b) of the oxygen consumption curves for the low-shore chitons, and its independence on temperature for the high-shore group, is another method by which the latter chiton group obtains an energetic advantage. The decrease in b with increasing temperature for both aerial and aquatic respiration implies that the metabolic rate of small chitons varies more with temperature changes than it does in large chitons (i.e., Q_{10} values for small chitons are larger than for large animals on the low shore).

Several studies have examined the influence of immersion and emersion on the respiration rates of marine invertebrates, and it has become apparent that there is no

clear rule relating shore level with respiration rates in air and water (Branch, 1981). It is likely that such relationships are linked to food availability, and hence, to whether an animal is an "exploiter" with a high turnover rate, or a "conserver" with low metabolism (Branch and Newell, 1978; Newell and Branch, 1980). High-shore *Sypharochiton pelliserpentis* exhibit the characteristics of "conservers", respiring more slowly in the medium in which they spend most time (i.e., air). Low-shore *S. pelliserpentis* respire faster in water, suggesting that they are not "conservers". However, their long lifespan, slow growth rate and low turnover are not characteristics of an "exploiter" (Newell and Branch, 1980). As both groups fed primarily during periods of immersion, it would be energetically advantageous for both groups to reduce their metabolic (and hence, respiratory) rates during the less gainfull emersion periods. Therefore, it seems likely that both groups are "conservers".

The activity pattern of high-shore *Sypharochiton pelliserpentis* varied seasonally due to its dependence on night length, and resulted in less activity during the summer. The metabolic energy savings of this behaviour are obvious. Daily activity patterns of both groups also act to conserve energy, as most feeding (and movement) is done while immersed, or in the cool of the night if emersed.

High-shore *Sypharochiton pelliserpentis* experience a higher mean environmental temperature than low-shore chitons, and while they exhibit various adaptations to reduce metabolic energy losses, the savings they gain are sufficient only to reduce their metabolic expenditure to 22% of total assimilated energy. The low-shore group lost 24% of its assimilation via respiration. While this explains some of the shortfall in consumption by high-shore chitons, it is clear that savings in some other areas are required also.

Defaecation

The calorific values of faeces obtained for *Sypharochiton pelliserpentis* are comparable with those given by Hughes (1971b) for three intertidal herbivorous gastropods of the genus *Nerita* (874, 1160 and 1202 J g^{-1}). Hughes (1971a) gave a value of 3296 J g^{-1} for faeces of the keyhole limpet, *Fissurella barbadensis*. Neither of Hughes's studies

reported the ash content of the faeces, but it seems likely, from descriptions in Bandel (1974), that relative to *Nerita*, faeces of *Fissurella* contained a high organic proportion which could explain their much higher calorific value. Paine (1971) found that faeces of another herbivorous gastropod, *Tegula funebralis*, were 13.3% organic, a proportion about twice as great as that found for *S. pelliserpentis*. Relative to other herbivorous molluscs, *S. pelliserpentis* appears to produce faeces with low organic content and low calorific value.

Seasonal trends in defaecation rates have been investigated rarely. Paine (1971) found that the gastropod *Tegula funebralis* exhibited no trends. On the other hand, Parry (1977) found that defaecation by *Cellana tramoserica* was strongly seasonal, with lowest faecal production in summer, and he related this to depressed standing stocks of algae. A similar, though less obvious, trend was exhibited by *Patelloida alticostata*, and the organic content of the faeces of this limpet rose during winter and spring, and was inversely related with the rate of faecal production (Parry, 1977). This inverse relationship suggested either more efficient absorption with a slow passage through the gut, or ingestion of food with a higher organic content during winter and spring. Faecal production rates for the mud snail *Ilyanassa obsoleta* were positively correlated with temperature (Edwards and Welsh, 1982), a trend shown also for two fresh water pulmonates (Calow, 1975b).

Faecal production by *Sypharochiton pelliserpentis* was clearly different at different shore levels. Yet, while low-shore chitons produced about twice as much faecal material as high-shore chitons, their actual consumption in terms of area of rock cleared was only about 20% greater. This indicates that high-shore animals either remove relatively less rock per rasp, or were able to assimilate a larger proportion of their inorganic intake. While some absorption of inorganic material consumed is possible (Crisp, 1971), it is highly unlikely that it represents a significant component of assimilation (Conover, 1966). A reduction in the quantity of rock ingested per rasp could provide an energetic advantage in terms of the reduction in metabolic demands of rasping, and a more efficient absorption due to the slower passage through the gut of smaller quantities of material. Assuming

that consumption by high-shore, compared with low-shore chitons included a smaller inorganic proportion, then the insignificant difference in ash proportion of faeces from both groups supports the conjecture of a higher assimilation efficiency on the high shore.

Differences in the activity of similar digestive enzymes between high- and low-shore groups of four acmaeid limpets were noted by Beppu (1968). If similar differences were shown for *Sypharochiton pelliserpentis*, then it would help explain shore level differences in assimilation efficiencies. The calculated assimilation efficiencies ($P+R+U:C_s$) suggest that high-shore chitons (93%) are relatively more energy efficient than the low-shore group (89%). Both these values compare well with efficiencies given by Branch (1981) for slow-growing, long-lived, "conserver" limpet species. However, they are much higher than all other A:C efficiencies shown in Table 17. This is due in part to inclusion of the large mucous production term (P_m) to A and C, but even if the P_m term is excluded from the efficiency calculations, values of about 70% are obtained and suggest that *S. pelliserpentis* minimises energy losses to a far greater degree (i.e., has a relatively smaller F component) than many other molluscs.

Efficiencies of individuals on both shore levels decrease with increasing body size. While this inverse relationship between size and efficiency is compatible with the relative reduction in metabolic energy requirements with growth (Zeuthen, 1953; Hemmingsen, 1960), other studies of molluscs have found no size-dependent variation in assimilation efficiencies (Ansell, 1982; Navarro and Winter, 1982).

Seasonal defaecation trends are difficult to explain. It was expected that extremes in consumption (maximum in February and minimum in August) would be reflected by faecal production. However, a phase delay of about three months was apparent, maximum defaecation being in May and the minimum in November. Once again, such a phase delay suggests either differential assimilation of inorganics (since faeces are approximately 94% inorganic) or variations in rock removed per radular rasp, on a seasonal basis. However, the first suggestion is unlikely (Conover, 1966), and no literature support for the second suggestion is available. Seasonal

variations in faecal calorific values, while faecal organic contents remain almost constant, imply different assimilation efficiencies throughout the year. Diatoms of different species can differ in their digestibility (Nicotri, 1977), and therefore, seasonal differences in stone-surface algal assemblages could result in variable assimilation efficiencies Increasing energy demands often associated with the breeding cycle can temporarily increase assimilation efficiencies (Ansell, 1982). Such a trend may be exhibited by *Sypharochiton pelliserpentis*, as lowest faecal calorific values (and hence, highest assimilation efficiencies) occurred in November during gametogenesis. In contrast, highest faecal calorific values occurred during the spent gonad phase in winter.

The link between assimilation efficiencies and consumption appears to be very complex and may depend on animal size and relative assimilability of inorganics, as well as on seasonal variations in diatom flora, metabolic and productive demands, and radular rasping technique. However, it is apparent that assimilation by high-shore chitons is more efficient than in the low-shore group.

Summary of energetic adaptations

It is likely that the high shore is a more physically stressful environment relative to the low shore, and that high-shore *Sypharochiton pelliserpentis* adapt in various physiological, structural and behavioural ways to reduce this stress (Horn, 1981, 1982). These adaptations, by reducing stress, would result in metabolic energy savings by high-shore chitons. However, it is clear that high-shore chitons are disadvantaged energetically, mainly because of feeding time restrictions which result in lower total energy consumption. If it is assumed that molluscs attempt to maximise P_r, and that successful reproduction is partly dependent on body growth and maintenance (P_g+P_m) (Branch, 1981), high-shore chitons should aim to reduce components of energy loss (i.e., R, F and U) or increase consumption.

High-shore chitons increased consumption by spending a greater proportion of their immersion and movement times feeding, relative to low-shore chitons. They lost a smaller proportion of energy via respiration as a result of reduced

temperature dependence of metabolism. Further, faecal production was much lower on the high than the low shore. The higher assimilation efficiencies of high-shore chitons could have been due to a slower passage of food through the gut, absorption of inorganics, or differences in the activities of digestive enzymes.

Both chiton groups studied appeared to be "conservers" (Newell and Branch, 1980), having slow growth, long life, and no overabundance of food. Migration from the low to the high shore appeared to be a response to density-dependent competition, and if so, suggests that the low shore is the preferred habitat, but that food there can become scarce enough to induce migration to a more physically stressful habitat. Further evidence for the additional stress experienced by high-shore chitons is provided by the seasonal calorific variation in somatic tissue. Whereas low-shore chitons appear to be able to build up storage products throughout the year for later use during gametogenesis, the calorific value of high-shore somatic tissue increased only during the winter at the time of a macroalgal bloom.

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APPENDIX 1

Computer programmes written for a Casio scientific calculator were used to calculate total annual consumption, respiration and defaecation for both chiton groups. The flowchart (Fig. 33) shows that the same general programme was used for all three components to account for changes in population structure throughout the year, using the population structure at January 1982 as a base.

The contents of the box marked * (Fig. 33) varied between programmes. For respiration, it involved the selection of the most appropriate weight:respiration relationship (Figs 20-23) depending on mean monthly temperatures. Also, the programme was run twice (once for aerial and once for aquatic respiration) and corrections were applied related to the proportion of time spent in air and water by animals of both groups. For defaecation, the relevant faecal production equation (Figs 26-27) was selected each month. As faecal production was measured only bi-monthly, the equation calculated for month x was used also for month x+1. Calculation of consumption took into account the temperature dependent equation for radular rasping rate (p. 26), the calculated relationship between body size and area cleared per rasp (Fig. 10), and the proportion of time spent feeding (Tables 1-2).

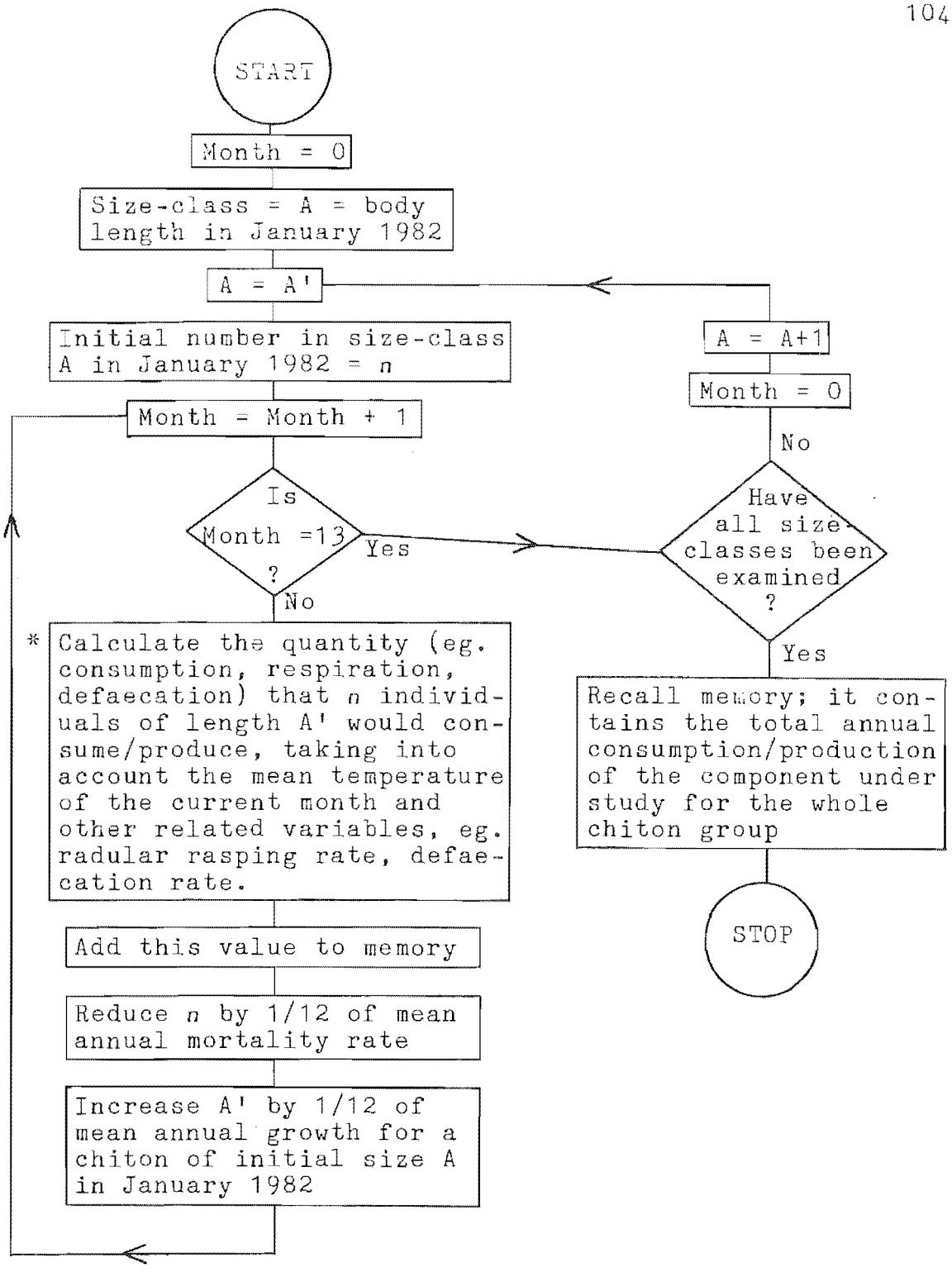

Fig. 33 - General flowchart used to construct computer programmes to calculate total annual consumption, respiration and defaecation by each chiton group.