

Reproductive Effort in Four Species of Intertidal Limpets

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Abstract

Reproductive effort was measured in 4 species of intertidal limpets: *Cellana tramoserica* (Sowerby) *Notoacmea petterdi* (Tenison Woods), *Patella peroni* Blainville and *Patelloida alticostata* (Angas) from south-eastern Australia. Field studies between 1971 and 1975 enabled indices of reproductive effort to be obtained using both gonad to body weight ratios and energy budgets. The ratio of annual gonad production to somatic tissue energy content is highest for *Patella peroni* (2.19). The ratios for *C. tramoserica* and *Patelloida alticostata* are lower but similar (1.02), and *N. petterdi* has the lowest ratio (0.78). The percentage of assimilated energy allocated to reproduction is also highest in *Patella peroni* (26.6%), but this index of reproductive effort is similar for the other three species (10.3 to 12.9%). Consequently, these 4 species are ranked in different orders with respect to “reproductive effort”, depending upon which index is used. However, the difference between both indices is small, and is less than has usually been anticipated. The difference is interpreted as being the result of the low metabolic rate of *N. petterdi* rather than as evidence for the inadequacy of one of the indices of reproductive effort.

Introduction

The concept of reproductive effort has assumed a central position in studies of life-history evolution since it was first elaborated by Williams (1966a, b). In Williams' original concept, both the expenditure of energy in reproduction and any increase in adult mortality which was associated with reproduction were considered to contribute to an organism's “reproductive effort”. Unfortunately, this concept proved difficult to quantify and, therefore, most

recent workers have followed the definition of reproductive effort suggested by Hirshfield and Tinkle (1975), i.e., “reproductive effort is ... that proportion of the total energy budget of an organism that is devoted to reproductive processes”.

Reproductive effort is usually measured as a ratio of gonad to somatic weight (or energy content), although measurements obtained using energy budgets are considered preferable (Hirshfield and Tinkle, 1975; Tinkle and Hadley, 1975; Grahame, 1977; Stearns, 1977; Atkinson, 1979). There are few studies in which reproductive effort has been measured using energy budgets; the only previous measurements being for lizards (Tinkle and Hadley, 1975), small mammals (Randolf *et al.*, 1977; Stenseth *et al.*, 1980), housemartins (Hails and Bryant, 1979) and flatworms (Woollhead and Calow, 1979). However, except for the limited data provided by Tinkle and Hadley (1975), and the laboratory studies of Calow and Woollhead (1977) and Woollhead and Calow (1979), there have been no studies in which reproductive effort has been measured using both energy budgets and ratios of gonad to body weight. In the present study, these two methods of measuring reproductive effort are compared for 4 species of intertidal limpets. In addition, these measurements of reproductive effort form the basis of a companion paper (Parry, 1982), in which the environmental factors responsible for the evolution of interspecific differences in reproductive effort are discussed.

Population energy budgets are used to measure reproductive effort, but this does not imply that selection operates upon populations rather than upon the individuals which comprise the populations (see also Williams, 1966a). Population “reproductive effort” should be proportional to the average individual reproductive effort. Furthermore, measurements of population reproductive effort can be simply made and provide a good basis for interspecific comparisons.

In several respects, limpets are well-suited to studies of reproductive effort. First, parental care, which makes the

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measurement of reproductive effort very difficult in studies of lizards, birds, and mammals (Ricklefs, 1977), is known to occur in only one species of limpet (Thorson, 1936), and does not occur in any of the species in the present study. Secondly complex courting behaviour, which may also complicate the measurement of reproductive effort in higher vertebrates, does not usually occur in limpets (Picken, 1980). Thus, in limpets, the energy devoted to reproduction is used almost entirely to produce gametes.

In addition, it is possible to construct reasonably accurate energy budgets for limpets in the field. Population respiration can be measured under almost natural conditions, as the flat rocky environment inhabited by limpets can be simulated realistically in the laboratory. Furthermore a "fast-moving" limpet does not consume much more oxygen than an inactive individual. Consequently, any difference between the levels of activity in the field and during laboratory measurements of oxygen consumption will only result in small errors when laboratory measurements are extrapolated to field conditions. The limited mobility of limpets and their abundance in an accessible rocky intertidal habitat also make them well-suited to population studies (Connell, 1972), i.e., growth and mortality rates can be accurately determined (see Parry, 1982).

Materials and Methods

The 4 species *Cellana tramoserica* (Sowerby), *Notoacmea petterdi* (Tenison Woods), *Patella peroni* Blainville and *Patelloida alticostata* (Angas) were chosen, as each was common within a different habitat. *N. petterdi* is restricted to the supralittoral zone, *C. tramoserica* and *Patelloida alticostata* occur in the midlittoral zone, and *Patella peroni* is largely confined to the sublittoral zone. Species from widely different zones were chosen for study as the differences between life-history parameters were more likely to be large.

Field studies were conducted near San Remo, 80 km south-east of Melbourne, Victoria, Australia between 1971 and 1975. The study sites are described in detail in Parry (1982).

Tissue Weight-Shell Length Regressions

At approximately monthly intervals, at least 20 individuals of each species were collected and maintained in aerated seawater for 3 d so that their gut contents were completely voided. Their shell lengths were measured to the nearest millimetre and the soft tissues removed. The gonad and somatic tissues were dissected apart, dried at 50 °C for 1 mo, and weighed. For each species and sampling date, regressions of log total tissue weight (*TW*) against log shell length (*L*), and log total somatic-tissue weight (*SW*) against log *L*, were then calculated.

Ash and Energy Content Determinations

Ash contents of tissues were measured by placing samples in a muffle furnace at 500 °C for 12 h. A microbomb calorimeter (modified after Phillipson, 1964) was used for all determinations of energy content.

The monthly samples of limpets used in the regressions of log *SW* against log *L* were also used for the determination of seasonal variation in ash content and energy content. Ash contents were determined each month, and the energy contents of somatic tissues were determined for females and males at approximately 3 mo (6 mo for *Patella peroni*) intervals. For each determination, at least 10 individuals were homogenised and the ash contents of 3 replicate samples and the energy contents of 4 replicate samples were measured.

The ash contents and energy contents of reproductive tissues were obtained by homogenising at least 20 ripe gonads of each sex.

Shell Weight-Shell Length Regressions

For each species, the relationship between shell weight and shell length was established by measuring and weighing between 65 and 80 shells.

Organic Content of Shell

The organic content of shell material was measured by dissolving the shell in dilute HCl, after Hughes (1970). Between 3 and 10 (depending upon the shell size) shells of each species were fragmented, and 3 replicate samples were dissolved in HCl.

Mathematical Relationship between Gonad Weight and Shell Length

The contributions of various size classes to the total reproductive output of a population depend on the relationship between gonad weight and shell length. Consequently, this relationship was investigated in detail for each species.

Each month, a minimum of 20 individuals of each species were collected, and during periods of active gonad growth weekly samples of 30 limpets of each species were collected. The shell length of each limpet was measured, the gonads were carefully removed, dried at 50 °C for 1 mo and weighed.

Preliminary graphical analysis for each species indicated that at all sampling times the relationship between gonad weight and shell length was close to linear beyond the shell length at which sexual maturity was attained. The length at sexual maturity for each species was obtained by using a technique for the analysis of coincident lines (Williams, 1959); the point of coincidence of a series of

lines is that point which minimizes the sum of squares of residuals of each line summed over all lines. The point of coincidence (length at maturity) of the regression lines of gonad weight against shell length was estimated for females and males separately, and was based on two assumptions:

- (1) Gonad weight (G) \propto shell length (S) – shell length at maturity (S_m)
i.e., $G = a(S - S_m)$
 $= aS'$
- (2) $G = bS' + cS'^2$,

where a , b and c are constants which change with reproductive condition.

Once the size at sexual maturity had been estimated for each species, the relationship between gonad weight and shell length was determined for data from each sampling date. The least-squares method was used to fit linear, quadratic, log-log and log-linear functions. The function which gave the best statistical fit between gonad weight and shell length varied between sampling times. Consequently, the function which gave the best overall fit for the year was determined by totalling the sums of squares of deviations over all sampling times.

Rates of Gonad Growth

The rate of gonad growth was measured for 3 yr for *Cellana tramoserica* (1972, 1973, 1974) and for 1 yr for *Notoacmea petterdi* (1973–1974), *Patella peroni* (1974–1975) and *Patelloida alticostata* (1974).

As the relationship between gonad weight and shell length was satisfactorily described by the linear relationship $G = aS'$ (see "Results – Reproductive Growth, P_r ") for each species, seasonal changes in gonad weight were estimated by plotting the gradient a in each regression of $G = aS'$ against the date on which the gonad sample was collected (see Parry, 1978, and present Figs. 4–6). The rate of gonad growth was obtained from weighted linear regressions of gradient a against time throughout the pre-spawning period. (Each point was weighted according to the number of gonads used in the regression, $G = aS'$ from which a was obtained.) The intersection of each weighted regression with the abscissa estimated the date of commencement of gonad production, and the gradient estimated the rate of gonad growth.

Measurements of Oxygen Consumption

Aerial respiration was measured using constant-pressure respirometers (see Parry, 1978). Aquatic respiration was measured using closed-system respirometers, each fitted with an oxygen electrode, which were immersed in a constant temperature bath ($\pm 0.2^\circ\text{C}$) of seawater (Parry, 1977).

Rates of oxygen consumption were measured in a laboratory situated 400 m from San Remo back beach. All limpets, except *Patella peroni*, were collected on a falling tide, and measurements of aerial oxygen consumption were completed during the period of the low tide in which the limpets were collected. Aquatic oxygen consumptions were measured during the period of the next high tide, at the same temperature, and with the same individuals used in the preceding measurements in air. However, measurements of aquatic oxygen consumption preceded measurements of aerial oxygen consumption for *P. peroni* (a subtidal species).

Aerial and aquatic oxygen consumptions were measured at regular intervals between July 1973 and September 1974 for *Cellana tramoserica* (Parry, 1978) and between February 1974 and February 1975 for *Patelloida alticostata*. The aerial oxygen consumptions of approximately 15 *C. tramoserica* and 10 *P. alticostata* were measured at 15°C (6-wk intervals), 20° and 25°C (3-mo intervals), 5° , 30° and 35°C (during the seasonal temperature extremes), and 10°C (3-mo intervals for *C. tramoserica* but only during winter for *P. alticostata*). The aquatic oxygen consumptions of approximately 15 *C. tramoserica* and 10 *P. alticostata* were measured at 3-mo intervals at either 10° , 15° or 20°C – whichever temperature was closest to the prevailing sea temperature at the time of the measurements.

The aerial oxygen consumptions of approximately 10 *Notoacmea petterdi* were measured at temperatures of 5° , 10° , 15° , 20° and 25°C during August 1979 and at temperatures of 20° , 25° , 30° and 35°C during February 1980. The aerial and aquatic oxygen consumptions of approximately 10 *Patella peroni* were measured at 10°C during August 1979 and the aerial oxygen consumptions of 10 *P. peroni* were measured at 20°C during February 1980.

In the field, *Cellana tramoserica* and *Patelloida alticostata* are usually inactive during low tide. Consequently, only those measurements of aerial oxygen consumption in which limpets were inactive were included in subsequent analyses. All measurements of aquatic oxygen consumption of *C. tramoserica* and *P. alticostata* were analysed, as both species were usually active to a similar extent in respirometers and when submerged in the field (Parry, 1977). All individuals of *Notoacmea petterdi* and *Patella peroni* were inactive during measurements of oxygen consumption.

For each species, regressions of log (aerial oxygen consumption) against log (dry tissue weight) and log (aquatic oxygen consumption) against log (dry tissue weight) were calculated for all temperatures and seasons.

Results

Somatic Growth, P_g

Covariance analysis revealed no significant seasonal change in the gradients of linear regressions of log total

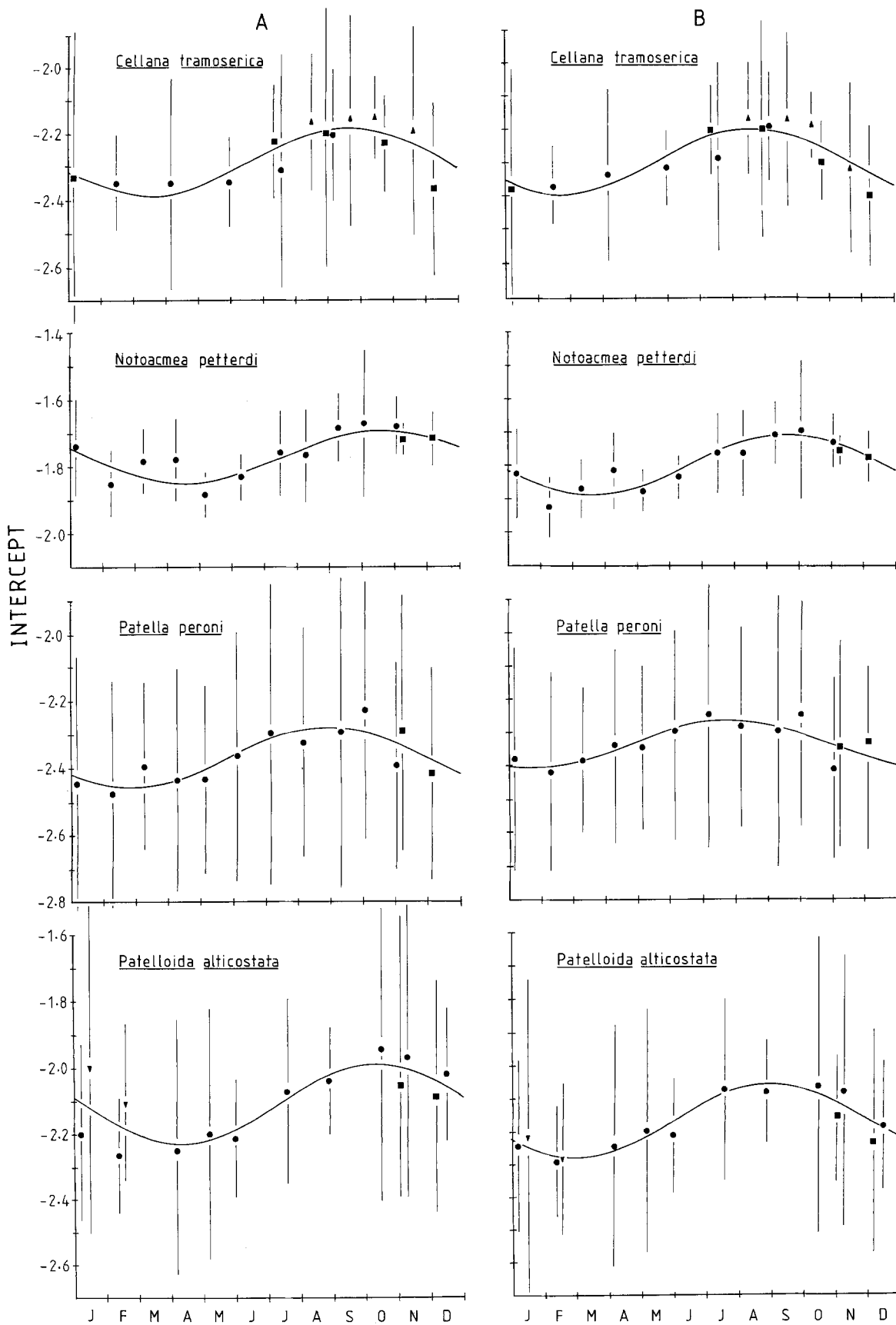


Fig. 1. Seasonal changes in values of intercepts (*A*, *B*) of regressions of log total tissue wt, $TW = A + (\text{gradient}) \log \text{shell length}, L$ and log somatic-tissue wt, $SW = B + (\text{gradient}) \log L$ for 4 species of intertidal limpets for: ▲, 1972; ■, 1973; ●, 1974; ▼, 1975. Equations of fitted curves are from Table 1. Error bars are 95% confidence limits (CL)

Table 1. Regression equations for dry total tissue weight (*TW*) and dry somatic weight (*SW*) against shell length (*L*) for 4 species of intertidal limpets, and equations describing seasonal variation in values of intercepts (*A*, *B*) of these equations. *D*=day of year, i.e., $1 < D < 365$, where *D*=1 on 1 January

Species	Log-log regression equation	Intercept of regression equation	
<i>Cellana tramoserica</i>	$\log TW = A + 3.43 \log L$	$A = -2.29 + 0.10 \sin [0.0172 (D + 195)]$	(<i>r</i> =0.84)
	$\log SW = B + 3.35 \log L$	$B = -2.30 + 0.10 \sin [0.0172 (D + 225)]$	(<i>r</i> =0.88)
<i>Notoacmea petterdi</i>	$\log TW = A + 2.85 \log L$	$A = -1.77 + 0.08 \sin [0.0172 (D + 164)]$	(<i>r</i> =0.87)
	$\log SW = B + 2.82 \log L$	$B = -1.80 + 0.09 \sin [0.0172 (D + 194)]$	(<i>r</i> =0.91)
<i>Patella peroni</i>	$\log TW = A + 3.67 \log L$	$A = -2.37 + 0.09 \sin [0.0172 (D + 217)]$	(<i>r</i> =0.85)
	$\log SW = B + 3.43 \log L$	$B = -2.34 + 0.07 \sin [0.0172 (D + 249)]$	(<i>r</i> =0.86)
<i>Patelloida alticostata</i>	$\log TW = A + 3.08 \log L$	$A = -2.11 + 0.12 \sin [0.0172 (D + 173)]$	(<i>r</i> =0.82)
	$\log SW = B + 3.08 \log L$	$B = -2.17 + 0.11 \sin [0.0172 (D + 214)]$	(<i>r</i> =0.93)

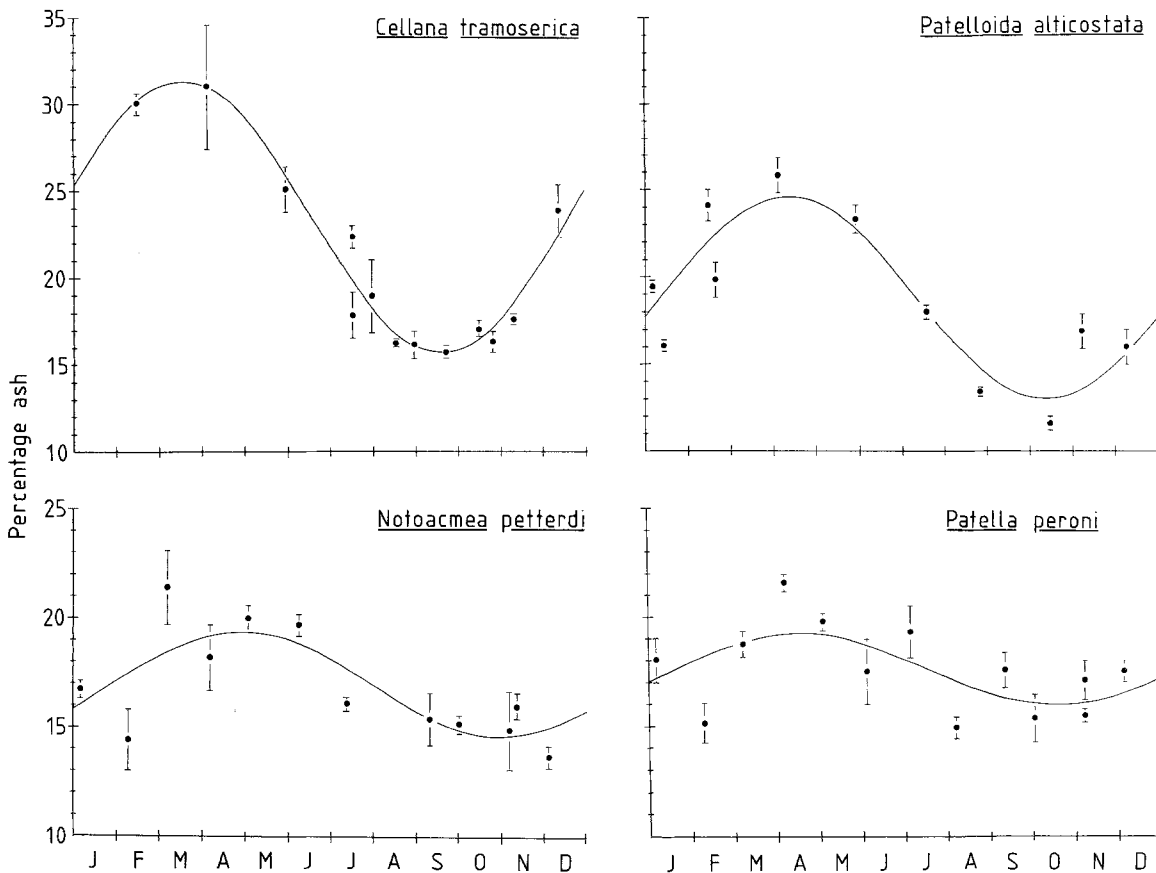


Fig. 2. Seasonal variation in ash contents of somatic tissues of 4 species of intertidal limpets. Equations of fitted curves are from Table 2. Error bars are 95% CL

Table 2. Equations describing seasonal variation in percentage ash and energy content of dry somatic tissue for 4 species of intertidal limpets

Species	Percentage ash	Energy content (EC)	
		(kJ ash-free g ⁻¹)	(kJ g ⁻¹)
<i>Cellana tramoserica</i>	% ash = $23.5 + 7.8 \sin [0.0172 (D + 13)]$	22.59	EC = $17.28 - 1.76 \sin [0.0172 (D + 13)]$
<i>Notoacmea petterdi</i>	% ash = $17.0 + 2.4 \sin [0.0172 (D + 335)]$	21.63	EC = $17.95 - 0.50 \sin [0.0172 (D + 335)]$
<i>Patella peroni</i>	% ash = $17.5 + 1.7 \sin [0.0172 (D + 349)]$	22.30	EC = $18.41 - 0.38 \sin [0.0172 (D + 349)]$
<i>Patelloida alticostata</i>	% ash = $18.8 + 5.8 \sin [0.0172 (D + 354)]$	22.93	EC = $18.62 - 1.34 \sin [0.0172 (D + 354)]$

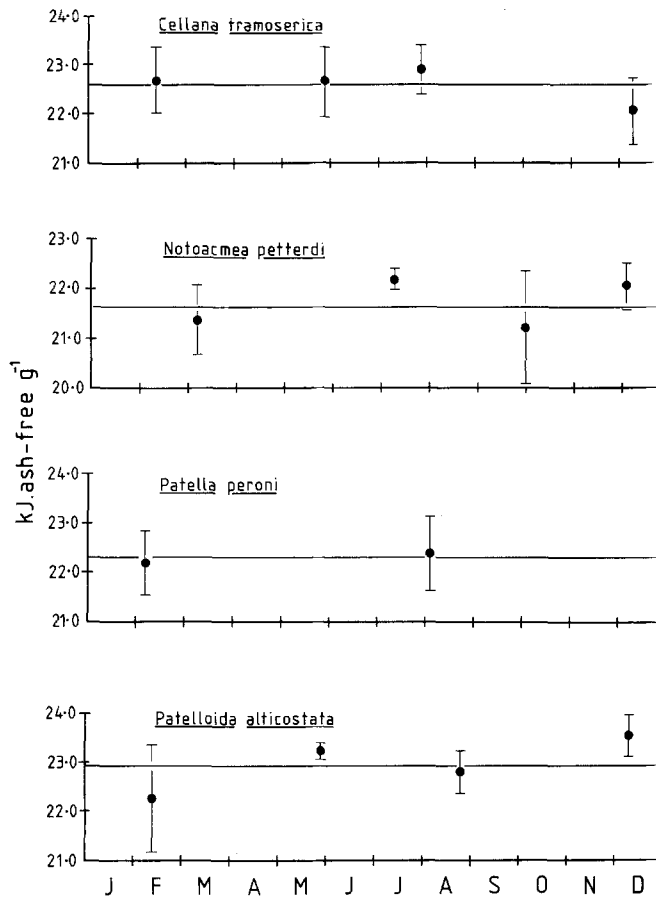


Fig. 3. Seasonal variation in energy content per ash-free gram of somatic tissue for 4 species of intertidal limpets. Errors bars are 95% CL

tissue weight (*TW*) against log shell length (*L*) or of log somatic-tissue weight (*SW*) against log *L* for *Cellana tramoserica*, *Notoacmea petterdi*, *Patella peroni* and *Patelloida alticostata*. Consequently, each regression was recalculated using the appropriate pooled gradient (Table 1). The intercepts of these recalculated regressions varied seasonally (Fig. 1), and sine functions, each with a wavelength of 1 yr, were fitted to describe these seasonal variations (Table 1). In general, these sine functions had higher correlation coefficients than third- and fourth-order polynomials which were also fitted.

Ash contents of the somatic tissues varied seasonally (Fig. 2), and these variations were described by fitting sine functions, each with a wavelength of 1 yr (Fig. 2, Table 2). These sine functions also had higher correlation coefficients than third- or fourth-order polynomials.

Seasonal variations in energy content were assumed to result from changes in ash content, as there was no significant seasonal change (ANOVA, $p > 0.05$ for each species) in the energy content of somatic tissues per ash-free gram for any of the species (Fig. 3). Thus, the expected seasonal variation in energy content per gram somatic tissue (Table 2) was calculated for each species from the mean energy content per ash-free gram of tissue (Table 2, Fig. 3) and the seasonal variation in ash content (Table 2, Fig. 2).

Reproductive Growth, *P_r*

Estimates of the shell length at sexual maturity, obtained by assuming a linear and a quadratic relationship between

Table 3. Shell length (cm) at sexual maturity for 4 species of intertidal limpets, assuming linear and quadratic relationships between gonad weight and shell length in females and males

Species	Females		Males		Average (both sexes)
	Linear	Quadratic	Linear	Quadratic	
<i>Cellana tramoserica</i>	2.47	2.32	2.32	2.33	2.36
<i>Notoacmea petterdi</i>	1.09	0.98	1.00	0.95	1.01
<i>Patella peroni</i>	2.69	2.53	2.50	2.33	2.51
<i>Patelloida alticostata</i>	1.53	1.62	1.59	1.68	1.61

Table 4. Sum of squares of deviations from regression lines, $G = f(S')$, totalled over all sampling dates for 4 species of intertidal limpets

Species	Linear	Quadratic	Log log	Log lin
Females				
<i>Cellana tramoserica</i>	1.4197	1.2029	1.4824	1.7668
<i>Notoacmea petterdi</i>	0.0223	0.0186	0.0234	0.0217
<i>Patella peroni</i>	5.0210	3.9164	5.2609	4.7477
<i>Patelloida alticostata</i>	0.1455	0.1365	0.1606	0.1642
Males				
<i>Cellana tramoserica</i>	0.9833	0.8995	1.0656	1.0238
<i>Notoacmea petterdi</i>	0.0287	0.0260	0.0298	0.0301
<i>Patella peroni</i>	1.2306	1.0296	1.4093	1.3473
<i>Patelloida alticostata</i>	0.0486	0.0438	0.0498	0.0552

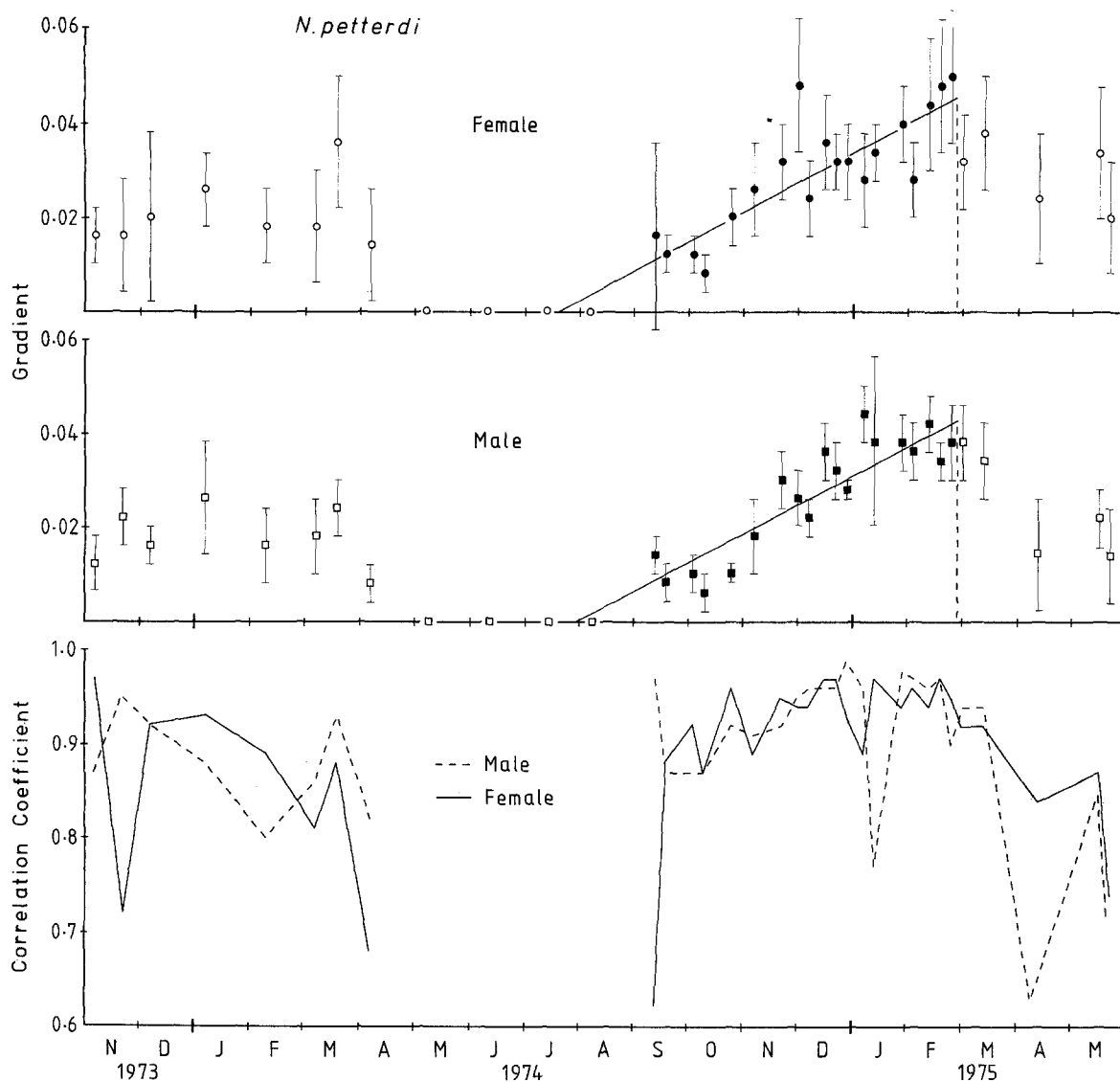


Fig. 4. *Notoacmea petterdi*. Seasonal changes in gradient a of the regressions of gonad weight (G) against shell length (S): $G = a(S - 1.01)$, for females and males. Filled symbols are data points used to calculate regression line of gradient a against time prior to spawning. Time of spawning is shown by vertical dashed lines. Error bars are 95% CL. Correlation coefficients of the equations $G = a(S - 1.01)$ for females and males are also shown

gonad weight and shell length, differed only marginally; and only small differences were apparent between females and males (Table 3). Thus, for each species, the average of the 4 estimates of shell length at maturity (Table 3) was used in subsequent calculations.

For each species, the quadratic relationship was found to best describe relationships between gonad weight and shell length (Table 4), but on only a few dates did the quadratic functions fit significantly better ($p < 0.05$) than the linear function (Table 5). Because of the simplicity of the linear function, and the small percentage of dates where curvilinearity was significant (Table 5), only the linear function was subsequently used.

Prior to spawning, the rate of growth of a gonad within a shell of a particular length remains constant (Parry, 1978, and present Figs. 4–6). This steady increase in gonad weight is followed by a rapid decrease in weight which corresponds to spawning (Parry, 1978, and present

Table 5. Incidence of curvilinearity in gonad weight and shell length relationship of 4 species of intertidal limpets

Species	Total no. of sampling dates	No. of sampling dates with significant ($p < 0.05$) curvilinearity	% of dates with significant curvilinearity
<i>Cellana tramoserica</i>			
♀	58	13	22
♂	59	4	7
<i>Notoacmea petterdi</i>			
♀	32	4	13
♂	32	2	6
<i>Patella peroni</i>			
♀	46	6	13
♂	45	5	11
<i>Patelloida alticostata</i>			
♀	31	3	10
♂	31	1	3

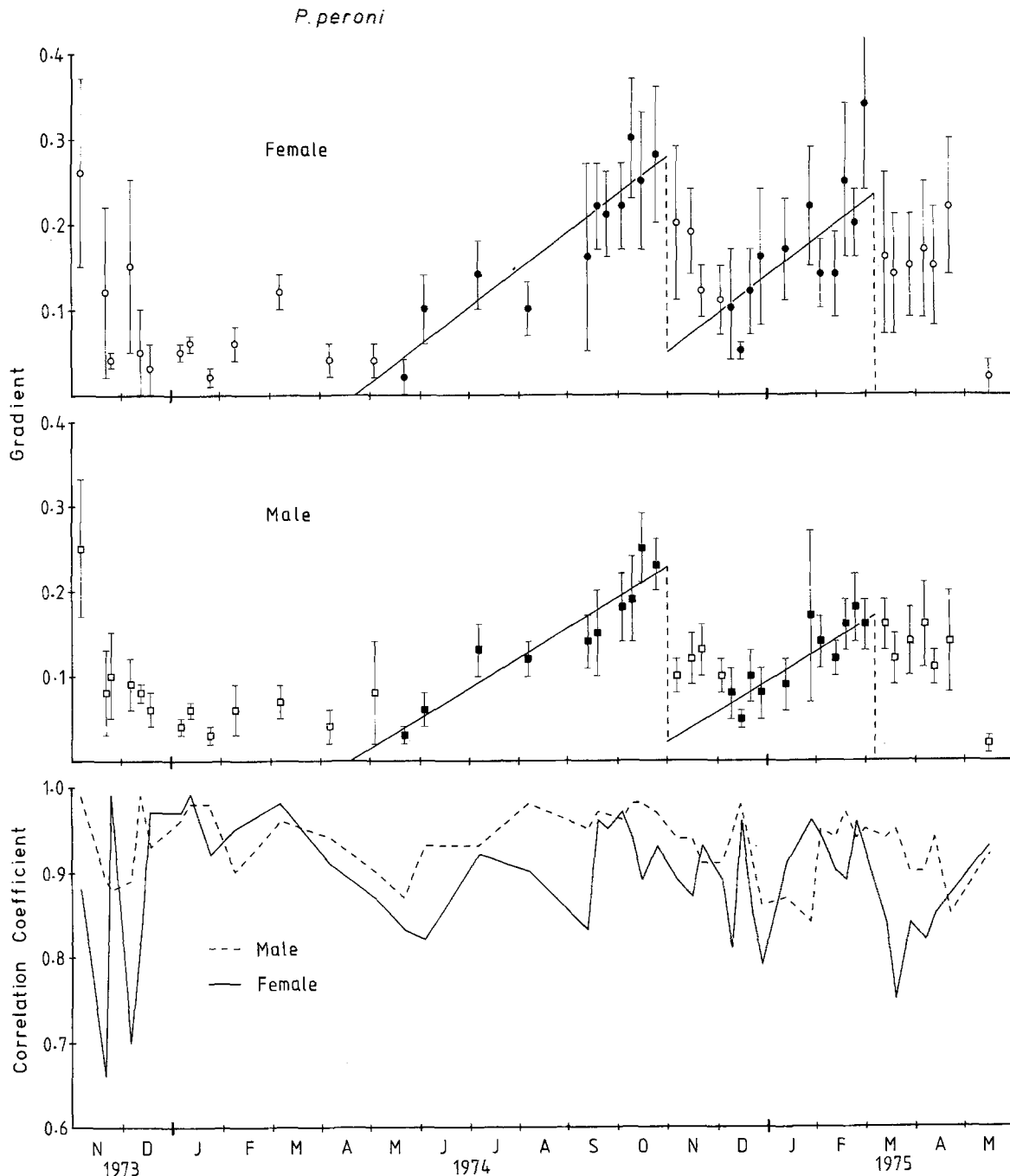


Fig. 5. *Patella peroni*. Seasonal changes in gradient a of the regressions of gonad weight (G) against shell length (S): $G = a(S - 2.51)$, for females and males. Correlation coefficients of regressions are also shown. Symbols as in Fig. 4

Figs. 4–6). The correlation coefficients of the equations: $G = aS'$ (Parry, 1978, and present Figs. 4–6) are usually high (> 0.9), except for the period immediately following spawning, when the population consists of limpets with a mixture of ripe and spent gonads.

One spawning was observed annually for all species except *Patella peroni*, where two spawnings were observed in 1974–1975 (Fig. 5). Histological changes in the ovary of *P. peroni* also suggest that this species spawns twice annually (Underwood, 1974).

Covariance analysis of the three lines representing gonad growth over 3 yr in *Cellana tramoserica* (Parry,

1978) indicated that the gradients of these lines did not differ significantly. Similarly, the two lines representing gonad growth during both spawnings of *Patella peroni* in 1974–1975 (Fig. 5) did not differ significantly in gradient. Consequently, for both species all lines were recalculated with the appropriate average gradient.

The total weight of gametes spawned annually by a limpet with a shell of particular length (gonad production per year, Table 6) was calculated from the rate and duration of gonad growth. The amount of energy to which this weight was equivalent (Table 6) was calculated from the measured energy content of ripe gonads (Table 7).

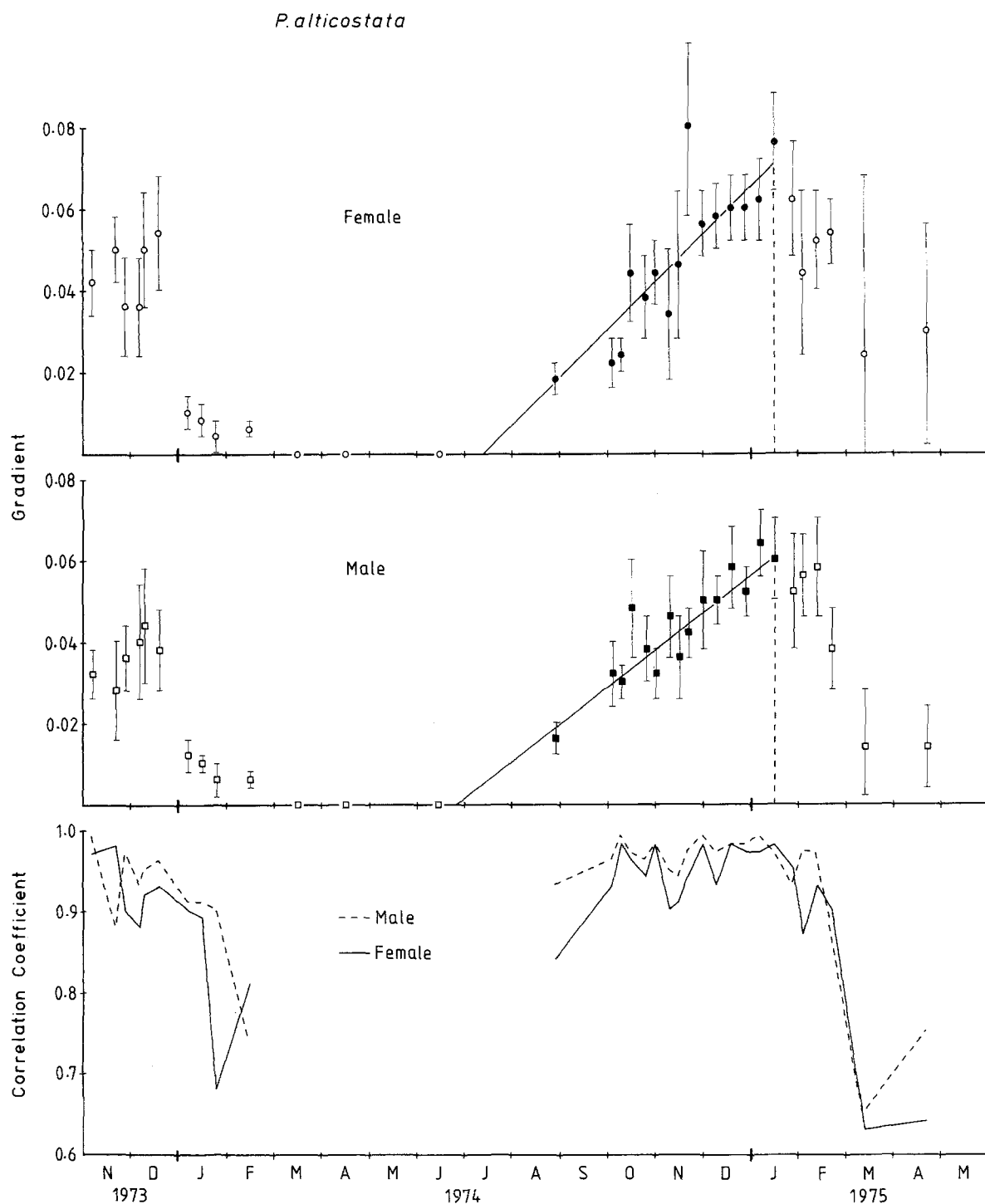


Fig. 6. *Patelloida alticostata*. Seasonal changes in gradient a of the regressions of gonad weight (G) against shell length (S): $G = a(S - 1.61)$, for females and males. Correlation coefficients of regressions are also shown. Symbols in Fig. 4

The estimated gonad production per year of females and males depends on the assumptions that (1) no spawning occurs during gonad development prior to the main spawning, and (2) after spawning gonad growth ceases entirely. Histological examination of the gonads of *Cellana tramoserica*, *Patella peroni* (Underwood, 1974) and other limpets (Orton *et al.*, 1956; Rao, 1973; Branch, 1974) provides some support for the first assumption, as relatively few mature eggs are available for spawning until gonads have reached nearly their full size. However the

second assumption is not supported by histological changes observed in the ovary of the limpet *Patella vulgata* (Orton *et al.*, 1956); in this species, spawning alternates with subsidiary bursts of development. Consequently, both assumptions above are approximations which are likely to cause the expenditure of energy in reproduction to be slightly under-estimated for all species.

Histological studies of *Cellana tramoserica* and *Patella peroni* (Underwood, 1974) indicate that neither of these species resorbs unshed oocytes.

Table 6. Summary of annual gonad production for 4 species of intertidal limpets of different shell lengths (S'), where $S' = S - S_m$; S = shell length, S_m = shell length at sexual maturity (all lengths in cm) for *Cellana tramoserica* (S'_{ct}), *Notoacmea petterdi* (S'_{np}), *Patella peroni* (S'_{pp}) and *Patelloida alticostata* (S'_{pa})

Species and breeding season	Rate of gonad development		Date of commencement of gonad development	Date of spawning	Duration of gonad development (d)	Gonad production yr ⁻¹		
	mg d ⁻¹	J d ⁻¹				mg	kJ	
<i>Cellana tramoserica</i> ($S'_{ct} = S - 2.36$)								
1972 - 1973	♀	1.04 S'_{ct}	27.57 S'_{ct}	3 Jul. 72	25 Nov. 72	145	151 S'_{ct}	4.004 S'_{ct}
	♂	0.787 S'_{ct}	16.07 S'_{ct}	25 Jun. 72	25 Nov. 72	153	120 S'_{ct}	2.452 S'_{ct}
1973 - 1974	♀	0.883 S'_{ct}	23.43 S'_{ct}	26 Jun. 73	14 Nov. 73	141	125 S'_{ct}	3.318 S'_{ct}
	♂	0.665 S'_{ct}	13.56 S'_{ct}	20 Jun. 73	14 Nov. 73	147	97.5 S'_{ct}	1.987 S'_{ct}
1974 - 1975	♀	0.802 S'_{ct}	21.25 S'_{ct}	28 Jun. 74	4 Jan. 75	190	153 S'_{ct}	4.058 S'_{ct}
	♂	0.870 S'_{ct}	17.78 S'_{ct}	21 Jul. 74	4 Jan. 75	167	146 S'_{ct}	2.983 S'_{ct}
Average of 3 seasons	♀	0.878 S'_{ct} *	23.30 S'_{ct}			159	140 S'_{ct}	3.715 S'_{ct}
	♂	0.795 S'_{ct} *	16.23 S'_{ct}			156	124 S'_{ct}	2.531 S'_{ct}
<i>Notoacmea petterdi</i> ($S'_{np} = S - 1.01$)								
1974 - 1975	♀	0.205 S'_{np}	5.06 S'_{np}	20 Jul. 74	26 Feb. 75	221	45.5 S'_{np}	1.125 S'_{np}
	♂	0.201 S'_{np}	3.89 S'_{np}	28 Jul. 74	26 Feb. 75	213	42.9 S'_{np}	0.828 S'_{np}
<i>Patella peroni</i> ($S'_{pp} = S - 2.51$)								
1974 - 1975 (1st breeding)	♀	1.44 S'_{pp}	35.86 S'_{pp}	21 Apr. 74	1 Nov. 74	193		
	♂	1.12 S'_{pp}	22.93 S'_{pp}	14 Apr. 74	1 Nov. 74	200		
1974 - 1975 (2nd breeding)	♀	1.99 S'_{pp}	49.54 S'_{pp}	1 Nov. 74	6 Mar. 75	126		
	♂	1.33 S'_{pp}	27.20 S'_{pp}	1 Nov. 74	6 Mar. 75	126		
1974 - 1975 (total)	♀	1.46 S'_{pp} *	36.36 S'_{pp}	21 Apr. 74	6 Mar. 75	319	466 S'_{pp}	11.60 S'_{pp}
	♂	1.18 S'_{pp} *	24.14 S'_{pp}	14 Apr. 74	6 Mar. 75	326	385 S'_{pp}	7.874 S'_{pp}
<i>Patelloida alticostata</i> ($S'_{pa} = S - 1.61$)								
1974 - 1975	♀	0.385 S'_{pa}	9.58 S'_{pa}	14 Jul. 74	15 Jan. 75	185	71.0 S'_{pa}	1.766 S'_{pa}
	♂	0.301 S'_{pa}	5.90 S'_{pa}	24 Jun. 74	15 Jan. 75	205	61.6 S'_{pa}	1.213 S'_{pa}

* These values are weighted average gradients resulting from covariance analysis of rates obtained by combining data from 3yr in the case of *C. tramoserica*, and 2 breeding seasons for *Patella peroni*

Table 7. Energy content of fully-developed pre-spawning gonads in 4 species of intertidal limpets

Species	No. of gonads/ homogenised. (No. of replicates)	kJ g ⁻¹ ± SE	% Ash ± SE	kJ ash free g ⁻¹ ± SE
Ovaries				
<i>Cellana tramoserica</i>	30 (4)	26.53 ± 0.32	5.9 ± 0.07	27.78 ± 0.21
<i>Notoacmea petterdi</i>	50 (4)	24.77 ± 0.23	10.4 ± 0.11	27.61 ± 0.27
<i>Patella peroni</i>	20 (4)	24.89 ± 0.11	7.6 ± 0.08	26.94 ± 0.13
<i>Patelloida alticostata</i>	20 (4)	24.89 ± 0.30	9.3 ± 0.09	27.41 ± 0.34
Testes				
<i>Cellana tramoserica</i>	40 (4)	20.42 ± 0.23	12.5 ± 0.06	23.30 ± 0.25
<i>Notoacmea petterdi</i>	70 (4)	19.33 ± 0.30	14.8 ± 0.15	22.68 ± 0.36
<i>Patella peroni</i>	20 (4)	20.46 ± 0.34	11.6 ± 0.03	23.18 ± 0.36
<i>Patelloida alticostata</i>	20 (3)	19.66 ± 0.06	12.6 ± 0.22	22.47 ± 0.07

Respiration, R

Covariance analysis indicated that the gradients of regressions of log (aerial oxygen consumption) against log (dry tissue weight) and log (aquatic oxygen consumption) against log (dry tissue weight) did not differ significantly

between seasons. Consequently, all regressions were recalculated with the average gradient for each species. The average gradients for *Cellana tramoserica*, *Notoacmea petterdi*, *Patella peroni* and *Patelloida alticostata* were 0.67 (±0.06, 95% confidence limits), 0.92 (±0.30), 0.79 (±0.31), and 0.55 (±0.10), respectively. For *C. tramo-*

serica and *P. alticostata* the intercepts (I) of these recalculated regressions varied seasonally and with temperature; the effects of these variables on aerial oxygen consumption are described by the following multiple-regression equations:

$$C. \textit{tramoserica}: \log R = I(D, T) + 0.67 \log W, \quad (1)$$

$$I(D, T) = 1.2202 + 0.12551 T - 0.44251 \times 10^{-2} T^2 + 0.64191 \times 10^{-4} T^3 - 0.14280 \times 10^{-2} D + 0.35302 \times 10^{-4} D^2 - 0.15312 \times 10^{-6} D^{-3} + 0.18442 \times 10^{-9} D^4 \quad (2)$$

($r = 0.990$),

$$P. \textit{alticostata}: \log R = I'(D, T) + 0.55 \log W, \quad (3)$$

$$I'(D, T) = 0.71874 + 0.14670 T - 0.51207 \times 10^{-2} T^2 + 0.70989 \times 10^{-4} T^3 - 0.13807 \times 10^{-2} D + 0.37593 \times 10^{-4} D^2 - 0.16760 \times 10^{-6} D^3 + 0.20551 \times 10^{-9} D^4 \quad (4)$$

($r = 0.978$),

where R = aerial oxygen consumption; W = dry tissue weight; T = temperature; D = day of year, $1 < D < 365$ (where $D = 1 = 1$ January).

The oxygen consumptions of average-sized *Cellana tramoserica* (0.25 g) and *Patelloida alticostata* (0.10 g) estimated from Eqs. (1) and (2), and (3) and (4), respectively, are shown in Fig. 7.

Differences between aerial and aquatic oxygen consumptions were tested by covariance analysis of pairs of regression equations obtained from measurements in air and seawater at the same temperature and during the same season. The aerial and aquatic oxygen consumptions of *Patella peroni* did not differ significantly. The aerial and aquatic oxygen consumptions of *Cellana tramoserica* and *Patelloida alticostata* only differed significantly during February 1974, when high levels of activity caused the aquatic respiration of both species to be higher than the aerial respiration (Parry, 1977). The high levels of activity shown by *P. alticostata* during measurements of aquatic oxygen consumption in Feb-

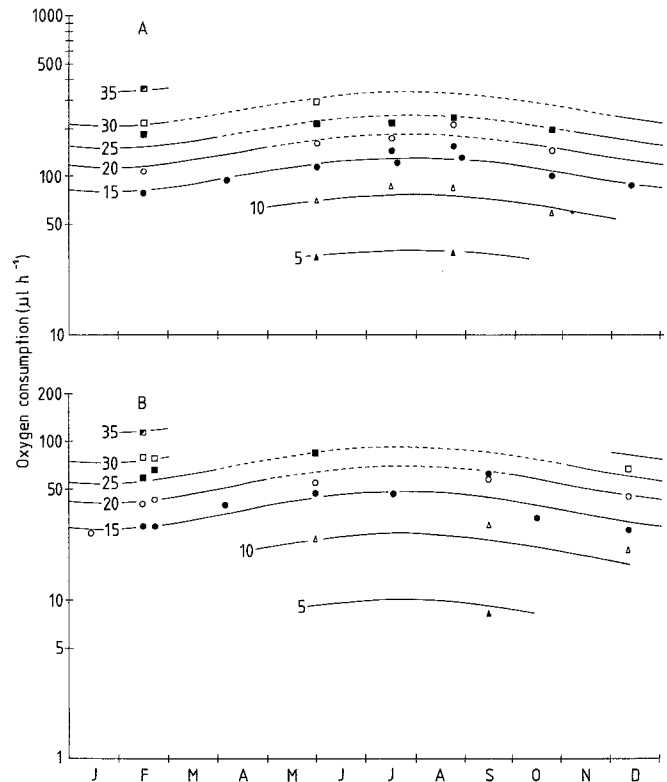


Fig. 7. *Cellana tramoserica* (A) and *Patelloida alticostata* (B). Seasonal changes in oxygen consumption predicted from Eqs. (1) and (2) for a 0.25 g *C. tramoserica* and from Eqs. (3) and (4) for a 0.10 g *P. alticostata* at 5°, 10°, 15°, 20°, 25°, 30° and 35°C. Dashed lines indicate oxygen consumptions predicted for temperatures above those that would be experienced in the field. Oxygen consumptions of a 0.25 g *C. tramoserica* estimated from Eq. (1) and for a 0.10 g *P. alticostata* estimated from Eq. (3) with the observed intercepts, I , for different temperatures are shown as: ▲ 5°C, △ 10°C, ● 15°C, ○ 20°C, ■ 25°C, □ 30°C, ▣ 35°C

ruary 1974 were not observed in the field at this time, nor were they observed during equivalent measurements in February 1975; consequently, rates of oxygen consumption of *P. alticostata* in air and seawater, measured at the same temperature, were assumed to be equal throughout

Table 8. Ratios of aerial oxygen consumption of 0.1 g individuals of *Notoacmea petterdi*, *Patella peroni* and *Patelloida alticostata* to aerial consumption of a 0.1 g *Cellana tramoserica*

Species and date	Temperature (°C)							Average
	5	10	15	20	25	30	35	
<i>N. petterdi</i>								
Aug.	0.58 ^a	0.29 ^a	0.75 ^a	0.49	0.50	ND	ND	} 0.48
Feb.	ND	ND	ND	0.30 ^a	0.49	0.36	0.51	
<i>P. peroni</i>								
Aug.	ND	0.71	ND	ND	ND	ND	ND	} ND
Feb.	ND	ND	ND	1.04	ND	ND	ND	
<i>P. alticostata</i>								
Aug.	0.53	0.61	0.66	0.69	0.69	ND	ND	} 0.65
Feb.	ND	ND	0.64	0.66	0.67	0.65	0.64	

^a These ratios are less accurate since low rates of oxygen consumption of *N. petterdi* approached limits of accuracy of the respirometers

the year. During February 1974, the aquatic oxygen consumption of *C. tramoserica* was 20% higher than the aerial oxygen consumption (Parry, 1977). Branch and Newell (1978) also found that the rates of oxygen consumption of three species of *Patella* were similar in air and seawater.

For each of the 4 species, aerial oxygen consumption of a 0.1 g limpet was calculated during winter and summer, at all temperatures for which data was available. The aerial oxygen consumptions of *Notoacmea petterdi*, *Patella peroni* and *Patelloida alticostata* were expressed as a ratio of the oxygen consumption of *Cellana tramoserica* under the same conditions (Table 8). *N. petterdi* consumed oxygen at 48% of the rate of *C. tramoserica* (Table 8). *Patella peroni* consumed oxygen at a lower rate than *C. tramoserica* during winter but at a higher rate than *C. tramoserica* during summer (Table 8). These differences may be due to the more seasonal growth of *C. tramoserica* compared with *P. peroni* (Parry, 1982). Consequently, the oxygen consumption of a 0.25 g *P. peroni* at 10 °C in winter, and at 20 °C in summer were both compared with the oxygen consumption of a 0.25 g *C. tramoserica* at these temperatures during winter. *P. peroni* consumed oxygen during both winter and summer at 65% of the rate of *C. tramoserica* during winter.

Construction of Population Energy Budgets

Annual Production and Mortality Estimates (*P*, *E*)

Production ($P = \Delta B + E$) was estimated for populations of *Cellana tramoserica*, *Notoacmea petterdi*, and *Patelloida alticostata* by the summation of annual changes in standing crop (ΔB) and annual losses due to mortality (E). E and ΔB were measured over 2 yr for *C. tramoserica* (between May 1971 and May 1973), *N. petterdi* (between November 1973 and November 1975), and *P. alticostata* (between December 1973 and December 1975), using the size-frequency distributions obtained on the study sites described by Parry (1982). Cohorts distinguished from these size-frequency distributions by Parry were considered separately. Thus "recruit" and "adult" cohorts were considered for *C. tramoserica* and *N. petterdi* and "recruit", "juvenile" and "adult" cohorts were considered for *P. alticostata*.

The standing crop of somatic tissue of each of these cohorts was calculated on the date of each size-frequency measurement, using the size-frequency distributions in Parry (1982), together with the somatic weight-shell length regressions (Table 1), and the somatic weight-energy content relationships (Table 2). The standing crop of the total (somatic and reproductive) tissue of the adult cohorts were also calculated on the same dates, using the same size-frequency data together with the total tissue-shell length weight regressions (Table 1) and the same somatic weight-energy content relationships (Table 2). Finally, the standing crop of shell material for each cohort was calculated on

Table 9. Regression equations for shell weight (*Sh W*) against shell length (*L*) for 4 species of intertidal limpets

Species	Equation	<i>r</i>
<i>Cellana tramoserica</i>	$\log Sh W = -1.410 + 3.54 \log L$	0.995
<i>Notoacmea petterdi</i>	$\log Sh W = -1.204 + 3.20 \log L$	0.929
<i>Patella peroni</i>	$\log Sh W = -1.262 + 3.22 \log L$	0.996
<i>Patelloida alticostata</i>	$\log Sh W = -1.192 + 3.25 \log L$	0.994

Table 10. Organic content of shell material in 4 species of intertidal limpets

Species	% organic content \pm SE
<i>Cellana tramoserica</i>	0.72 \pm 0.04
<i>Notoacmea petterdi</i>	0.71 \pm 0.09
<i>Patella peroni</i>	0.15 \pm 0.01
<i>Patelloida alticostata</i>	0.47 \pm 0.04

the same dates using the same size-frequency data, the shell weight-shell length regressions (Table 9), and the measured organic contents of shell material (Table 10), which was assumed to have the same energy content as protein (17.1 kJ g⁻¹; White *et al.*, 1968).

In general, the losses of energy through mortality ($E = \Delta N \cdot \bar{w}$) were estimated from the decrease in the number of individuals in each cohort (ΔN), and the average energy content of members of the cohort (\bar{w}) during the period between size-frequency determinations. The total losses of energy ($E_{tot} = \Delta N \cdot \bar{w}_{tot}$) and the losses just through somatic tissues ($E_{som} = \Delta N \cdot \bar{w}_{som}$) were estimated for the adult cohorts of *Notoacmea petterdi* and *Patelloida alticostata* by considering the energy content at death to be either the average total tissue energy content (\bar{w}_{tot}) or the average somatic tissue energy content (\bar{w}_{som}). E_{som} and E_{tot} for the adult cohorts of *Cellana tramoserica* were calculated directly from size-frequency distributions of mortality (Parry, 1982) and the appropriate information in Tables 1, 2, 9 and 10.

The mortality of the adult cohort of *Patelloida alticostata* during 1975 was calculated by assuming that the average energy content at death during 1975 was the same as during 1974. The energy contents of *Notoacmea petterdi* which migrated into the study area (Parry, 1982) were assumed to equal the mean energy content of individuals on the study area during the interval in which the population size increased.

Frequent size-frequency measurements of sub-tidal populations of *Patella peroni* were not possible, hence the production of *P. peroni* was estimated from its rate of turnover. The average standing crops of total and somatic tissues of a population of *P. peroni* were estimated from the size-frequency distribution of *P. peroni* at Site C in Parry (1982) and the appropriate information from Tables 1, 2, 9, and 10. As the mean annual adult mortality rate of *P. peroni* is 50% (Parry, 1982), the annual losses of

total tissues (E_{tot}) and somatic tissues (E_{som}) were assumed to equal half of the respective standing crops.

Estimates of production (P) and mortality (E) for each of the species are summarized in Table 11.

Energy Spawned Annually, G

The annual amount of energy spawned (G) at each study site (Table 11) was calculated from the average gonad production per year of females (Table 6) and the size-frequency distribution of the population at each study site at the time of spawning (Parry, 1982).

Population Respiration

The oxygen consumed by populations of *Cellana tramoserica* and *Patelloida alticostata* at their respective study sites (Parry, 1982) were calculated monthly for each year that populations were studied. The size-frequency distributions of the populations at the midpoint of each month were calculated by linear interpolation from 6-wk size-frequency distributions (Parry, 1982). The weight of individuals of each shell length was calculated from the equations in Table 1.

The aerial and aquatic oxygen consumptions of each individual were calculated from Eqs. (1) and (2) (*Cellana tramoserica*) and Eqs. (3) and (4) (*Patelloida alticostata*). The temperatures of limpets when submerged were presumed to be the same as the mean monthly sea temperatures at Point Lonsdale (King, 1970), 50 km west of San Remo. During January, February and March, the aquatic oxygen consumption of *C. tramoserica* obtained from Eqs. (1) and (2) was multiplied by 1.2 to allow for the increased oxygen consumption associated with the increased activity of this species during summer.

The time and duration of each aerial exposure was calculated from the predicted times and heights of tides (Ports and Harbours, Victoria, 1971–1975). The average temperature during each exposure was calculated by averaging three air temperatures, namely those obtained at the time of emergence, at the time of low tide, and at the time of submergence. These three temperatures were estimated from the daily temperature extremes at Cape Schanck, 35 km west of San Remo.

The oxygen consumption of *Notoacmea petterdi* and *Patella peroni* populations on their study sites (Parry, 1982) were calculated in a similar way to those of *Cellana tramoserica* and *Patelloida alticostata*. *N. petterdi* were usually splashed by waves when the tide was about the mid-tidal level. Consequently, *N. petterdi* were assumed to be exposed to air temperatures and sea temperatures for half of each month. The oxygen consumption of each individual *N. petterdi* was calculated using Eqs. (1) and (2), which were then multiplied by 0.48 (Table 8). The *Patella peroni* study site was continually subject to sea temperatures, and the oxygen consumptions of individual

Table 11. Summary of energy budget parameters (units = kJ m²), energy conversion efficiencies, and reproductive effort for 4 species of intertidal limpets. Where possible, symbols follow International Biological Programme recommendations (Petrušewicz and Macfadyen, 1970): ΔB = change in biomass; E = loss of tissue through mortality (subscripts *som*, *rep* and *tot* refer to losses of somatic, reproductive and both tissues combined, respectively; P_g = somatic growth; G = energy spawned; P_{rep} = reproductive growth; P = production; R = respiration; and A = energy assimilated

Species and dates	ΔB	E_{tot}	E_{som}	E_{rep} ($E_{tot-som}$)	P_g ($\Delta B + E_{som}$)	G	P_{rep} ($G + E_{rep}$)	P ($P_{rep} + P_g$)	R	A ($P + R$)	Conversion efficiencies		Maximum ratio of annual ovary pro- duction : minimum somatic tissue energy content*
											Net growth $\frac{P}{A}$	Repro- ductive effort $\frac{P_{rep}}{P}$	
<i>Cellana tramoserica</i>													
May 1971 – May 1972	1.17	15.65	13.68	1.97	14.85	36.99	38.95	53.81	248.95	302.75	17.8	12.9	} 1.02
May 1972 – May 1973	-7.41	22.34	19.46	2.89	12.05	31.34	34.23	46.28	256.90	303.17	15.3	11.3	
<i>Notoacmea petterdi</i>													
Nov. 1973 – Nov. 1974	7.82	10.38	10.38	0.00	18.20	51.80	51.80	70.00	397.57	449.57	15.6	11.5	} 0.78
Nov. 1974 – Nov. 1975	4.10	ND	-3.81	ND	0.29	ND	ND	ND	400.28	ND	ND	ND	
<i>Patella peroni</i>													
1974 – 1975	0	112.5	90.8	21.8	90.8	259.0	280.8	371.5	682.4	1 053.9	35.3	26.6	2.19
<i>Patelloida alticostata</i>													
Dec. 1973 – Dec. 1974	-1.26	4.64	4.14	0.54	2.89	4.60	5.15	8.03	41.71	49.74	16.1	10.3	} 1.02
Dec. 1974 – Dec. 1975	0.63	2.89	2.59	0.29	3.22	5.06	5.36	8.58	ND	ND	ND	ND	

* From Fig. 8

P. peroni were calculated from the oxygen consumption of *C. tramoserica* during winter (August) and the estimates multiplied by 0.65.

The annual metabolic heat losses of populations (*R*, Table 11) were calculated by assuming an energy equivalent of $14.1 \text{ J mg}^{-1} \text{ O}_2$ (Elliott and Davison, 1975).

Estimates of Reproductive Effort

Ratios of annual gonad production to minimum somatic tissue energy content for each species (Fig. 8) were calculated from the somatic weight-shell length relationships (Table 1, Fig. 1) and the gonad production-shell length relationships (Table 6). These ratios increase with shell length to a maximum value and then decrease (Fig. 8). These decreases probably occur because the equations from which the ratios are derived are increasingly inaccurate at large shell lengths. Consequently, the maximum values of these ratios have been taken as a measure of "reproductive effort" (Table 11). The ratio of maximum annual gonad production to minimum somatic tissue energy content is highest for *Patella peroni* (2.19, Table 11). The ratios for *Cellana tramoserica* and *Patelloida alticostata* are similar but lower (1.02, Table 11), and *Notoacmea petterdi* has the lowest ratio (0.78, Table 11).

Estimates of reproductive effort $\frac{P_{\text{rep}}}{A}$, obtained by using energy budgets, indicate that *Patella peroni* also allocates the highest (26.6%, Table 11) percentage of assimilated energy to reproduction. The other 3 species allocate similar but smaller amounts of energy to reproduction (10.3 to 12.9%, Table 11). Consequently, these 4 species are ranked by both indices in the same order, except that *Notoacmea petterdi* appears to allocate a similar proportion of assimilated energy to reproduction as *Cellana tramoserica* and *Patelloida alticostata*, but to have a lower gonad to body ratio than these two species.

Discussion

Reproductive effort has been measured for limpets, using gonad to body weight ratios, by Branch (1974), Choat and Black (1979) and Picken (1980). The values obtained by Choat and Black and by Picken, both of whom used dry weights, are similar to those obtained in the present study for *Cellana tramoserica*, *Notoacmea petterdi*, *Patella peroni* and *Patelloida alticostata* (also, Parry, 1982), but those obtained by Branch are substantially lower, probably because he used wet weights. Branch (1974) also concluded that male limpets may devote more energy to reproduction than females; whereas the results of the present study would suggest the opposite (Table 6). Again, this difference may be due to his use of wet weights rather than energy contents. The energy content of an ovary may be higher than that of a testis, despite the testis having a higher wet weight. The energy content per unit dry weight is higher for the ovary than the testis (Table 7) and, as male limpets have higher moisture contents than female limpets (Suryanarayanan and Balakrishnan, 1976), the testis may also have a higher moisture content.

The maximum values of the ratios of annual ovary production to minimum tissue energy content (Fig. 8, Table 11) suggest that "reproductive effort" decreases in the sequence *Patella peroni* > *Cellana tramoserica* ~ *Patelloida alticostata* > *Notoacmea petterdi*. Estimates of reproductive effort based on energy budgets suggest an identical sequence, except that the reproductive effort of *N. petterdi* appears to be similar to, rather than lower than, that of *C. tramoserica* and *P. alticostata* (Table 11). The difference obtained between these two sequences is small in contrast to the expectations of many authors (see "Introduction"), and suggests that previous criticisms of gonad to body ratios should be reconsidered.

Gonad to body ratios have been regarded as unsatisfactory measures of reproductive effort for four reasons: (1) Gonad to body ratios usually increase allometrically

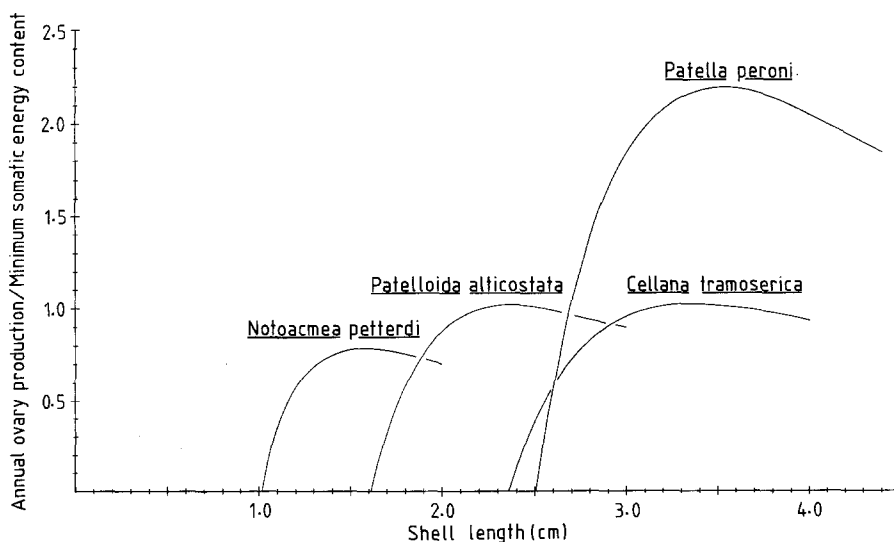


Fig. 8. Ratio of annual ovary production to minimum somatic tissue energy content plotted against shell length for 4 species of intertidal limpets

with adult size, but such effects are seldom considered (Kaplan and Salthe, 1979). (2) Differences in gonad to body ratios may merely reflect the volume constraints imposed by different body shapes which are the result of selection for different ecological roles (Vitt and Congdon, 1978). (3) Species may differ in the number of clutches laid per annum (Hirshfield and Tinkle, 1975). (4) Individuals of two species could devote the same quantities of energy to reproduction at equivalent body sizes, but differ in the amount of energy gathered or in the time during which it was gathered (Hirshfield and Tinkle, 1975).

The first three of these criticisms have been explicitly considered in this study or do not apply to limpets. Gonad to body ratios increase with shell length following the attainment of sexual maturity, but approach a maximum value at large shell lengths for each species (Fig. 8). Similarly, the proportion of body weight invested in gonads is independent of shell length in all but the smallest adults in the Antarctic limpet *Nacella concinna* (Picken, 1980). The absence of an allometric increase in gonad to body weight ratios (or fecundity to body weight ratios) is not uncommon in invertebrates (see Spight and Emlen, 1976, review; and Browne, 1978; Brown, 1979). Thus, while the possibility of allometric changes in gonad to body weight ratios should always be considered (Kaplan and Salthe, 1979), such changes need not occur.

The second criticism is most important when the species being compared are taxonomically and/or ecologically different. The four species of limpets in the present study are taxonomically related (2 acmaeids, 2 patellids) and they are ecologically similar, at least compared with the lizards considered by Vitt and Congdon (1978). Differences between the shell shapes of the four species are small (own unpublished data), and are not obviously related to tidal height or wave action.

The third criticism of gonad to body ratios is easily avoided by weighting ratios according to the number of spawnings which occur annually (Hirshfield and Tinkle, 1975). In the present study, the ratio of annual gonad production to body weight explicitly incorporates a weighting for the annual number of spawnings.

Hirshfield and Tinkle (1975) argue that there are situations in which species may have identical reproductive efforts but differ in their gonad to body ratios. The present study confirms their prediction. *Notoacmea petterdi* has a similar reproductive effort to *Cellana tramoserica* and *Patelloida alticostata* (Table 11), yet the gonad to body ratio of *N. petterdi* is lower than that of the other two species (Fig. 8, Table 11). However, except for *C. tramoserica*, complete energy budgets were only measured for each species for 1 yr, and the measurement of reproductive effort for *N. petterdi* may not be representative. The reproductive effort of *N. petterdi* was measured only during 1973–1974, but it seems certain that reproductive growth would have been considerably lower during 1947–1975. The amount of somatic growth during 1973–1974 was more than 50 times greater than during 1974–1975 (Table 11). However, it is clear why the repro-

ductive effort of *N. petterdi* during 1973–1974 appears high compared with the gonad to body ratio. If we let the average gonad to body ratio equal $\frac{P_{rep}}{\bar{B}}$ (where P_{rep} is the energy devoted to reproduction and \bar{B} is the average biomass), then this ratio will usually be correlated with reproductive effort $\frac{P_{rep}}{A} = \frac{P_{rep}}{P+R} = \frac{P_{rep}}{P+r\cdot\bar{B}}$ (where R = population respiration, r = average metabolic rate), as the denominator of both ratios is dominated by \bar{B} . When comparing between two species, A and B , one circumstance in which $\frac{P_{repA}}{\bar{B}_A} > \frac{P_{repB}}{\bar{B}_B}$ but $\frac{P_{repA}}{P_A+r_A\bar{B}_A} < \frac{P_{repB}}{P_B+r_B\bar{B}_B}$ occurs when r_A is substantially lower than r_B . The low metabolic rate of *N. petterdi* compared with *C. tramoserica* (Table 8) explains the similarity of their reproductive efforts (Table 5) despite *N. petterdi* having a lower gonad to body ratio (Table 11, Fig. 8).

However, an exact statement of the relationship between reproductive effort and gonad to body ratios does not seem possible at present (see also Hirshfield and Tinkle, 1975). In part this results, despite the emergence of some patterns in the interrelation between energy budget parameters (Humphreys, 1979) and energy budget and life-history parameters (Waters, 1977; Robertson, 1979), from our ignorance of the physiological constraints and life-history tradeoffs which limit the possible combinations of growth, reproduction and respiration in an energy budget. In particular, the need for a better understanding of those factors which determine rates of metabolism in different species is emphasized.

Clearly, measurements of reproductive effort using energy budgets constitute a better empirical basis than gonad to body ratios for understanding differences in energy partitioning. However, gonad to body ratios contain important information that cannot be as easily deduced from energy budgets. For example, there is clearly a maximum amount of gonad which an adult can maintain without greatly jeopardizing its future survival, and this may be of importance in determining the frequency of reproduction. Size constraints probably explain why *Patella peroni* spawns twice annually. At large shell lengths, limpets spawn 40 to 60% of their total energy content each spawning (calculated from last column of Table 11). Similarly, the ovary comprises up to 70% of the dry tissue weight of the limpet *Acmaea insessa* (Choat and Black, 1979). As large individuals of *P. peroni* spawn the equivalent of more than their total energy content annually (last column, Table 11), this very large energy expenditure could not be achieved in a single spawning.

The present study indicates that indices of reproductive effort based on gonad to body ratios and on energy budgets may differ, but that these differences need not be large. Indeed, even where differences between both types of indices occur, it is not clear that this should be considered evidence that one of the indices is an inappropriate measure of "reproductive" effort rather than evi-

dence for different strategies of energy allocation, which may be only indirectly related to reproduction.

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