

Growth and Production of Mussels *Mytilus edulis* from Two Populations

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ABSTRACT: Gompertz growth curves for *Mytilus edulis* (L.) from two populations were derived from size-class analysis. By the incorporation of time and temperature as day-degrees, and of the results of length/dry weight regressions, estimates were made of seasonal changes in weight, and of fecundity as mantle weight loss on spawning. The results agreed well with independent estimates of growth made by integrating the results of physiological measurements of energy balance. Differences between production estimates for individual mussels at the two sites are discussed and related to various physiological differences, chiefly the seasonal pattern of the efficiency of absorption of energy from the ingested ration. Somatic production is shown to be similarly dependent on temperature in both populations, but seasonally abnormal temperatures and a reduced quality of available food at one site caused a marked reduction in the production of gametes.

INTRODUCTION

Many marine mussels of the genera *Mytilus*, *Choromytilus*, *Aulacomya* and *Perna* combine a tolerance to a wide range of environmental conditions with a flexibility of physiological response, reflected in various rates and seasonal patterns of growth, in such a way as to facilitate comparisons of the production potential of different habitats. Comparisons of rates of growth of mussels from different geographical areas have been made by Theisen (1968, 1973) in Denmark and Greenland, by Seed (1973) and Dare and Edwards (1976) in the United Kingdom, by Freeman and Dickie (1979) in Canada, Hickman (1979) in New Zealand, and by Berry (1978) and Griffiths and King (1979) in South Africa.

Estimates of the growth rates of bivalve molluscs are made by analysing annual growth rings, by measurement of marked individuals, by the analysis of size-classes in the population, or by a combination of these procedures. Each of these methods has its own advantages and disadvantages (Haskin, 1954; Seed, 1976). More recently, Lutz (1976) has described a direct technique for age determination of mussels using acetate peels of polished and etched longitudinal sections of the shell (see also Jones et al., 1978; Lutz and Castagna, 1980). In a wide-scale study of mussel growth, size-class analysis combined with direct age determination of a sub-sample is probably the pre-

ferred method since annual shell rings are often indiscernible in these species and mark/recapture methods are very labour-intensive. However, size-class analysis proves difficult in some circumstances, where recruitment is prolonged in time, with inevitable merging of the age-classes. Even when this type of analysis is possible, it results in a statement of average growth of individuals in the population and obscures individual variability which, if genetically based (Milkman and Koehn, 1977; Innes and Haley, 1977) can make the deduction of environmental correlates of growth difficult (Freeman and Dickie, 1979).

Whatever the method of estimating growth in bivalves, the results are usually described by means of a von Bertalanffy or a Gompertz growth equation (Ricker, 1975). Both equations were used by Theisen (1973), who concluded that the sigmoidal Gompertz curve described the growth of *Mytilus edulis* from Greenland to about half the maximum shell length, whereas the Bertalanffy equation was valid for sizes larger than one-third the maximum length. Both these growth models have the advantages over more empirical best-fit equations of some generality and common usage, facilitating comparisons between populations, particularly when calculated to include variance estimates for the parameters (Bayley, 1977). However, caution is necessary when attempting comparisons based only on individual parameter values (Hankioja and Hakala, 1979).

An alternative procedure for estimating growth is based on the energy balance equation of Winberg (1960). Measurement of the various components of the energy budget provide an estimate of growth potential or scope for growth (Warren and Davis, 1967; Bayne et al., 1976) which, when integrated over time and applied to individuals of different sizes, can be used to derive an average growth curve. Physiological estimates of growth allow inter- and intra-population comparisons of the components of growth, such as differences in the processes of energy gain and loss.

The aims of the present paper are to compare the results of two methods of growth estimation – by size-class analysis and by physiological measurements – in two populations of *Mytilus edulis*, and to identify any differences in the main components of growth at two ecologically different sites. Most of the physiological data are taken from the study reported by Bayne and Widdows (1978).

MATERIAL AND METHODS

Mytilus edulis (L.) were sampled from two sites near Plymouth (England). The first, called the Lynher site, is situated at the confluence of the Lynher and Tamar estuaries; the second, the Cattewater site, is situated at the cooling-water outfall of a small electricity-generating station in the estuary of the Plym (Bayne et al., 1977; Bayne and Widdows, 1978). At both sites samples were collected between mean low water of spring and neap tides where the mussels were exposed to air for an average four hours per day. The samples for size-frequency analyses were taken monthly between June 1973 and August 1974 (Lynher) and September 1973 and December 1974 (Cattewater) by random 0.1 m² quadrats, the contents of which were sorted through 2 mm and 0.5 mm mesh sieves to collect all mussels except the smallest post-larval recruits.

All mussels from each quadrat were measured for shell length (maximum antero-posterior dimension). Twenty-five individuals, including all sizes represented in the quadrat, were taken for separate measurements of mantle and non-mantle tissue weights after drying at 90 °C for 24 h. A further 10 individuals were used for analysis of the energy value of mantle and non-mantle tissues separately using a Phillipson micro-bomb calorimeter.

The measurements of shell length were grouped into 5-mm classes and all the resulting length/frequency tables resolved into Gaussian components using the method of Bhattacharya (1967). Figure 1 shows the degree of separation of component distributions that was possible. A thorough study of all available data resolved 6 size-classes; we make the assumption that these size-classes represent separate age-classes.

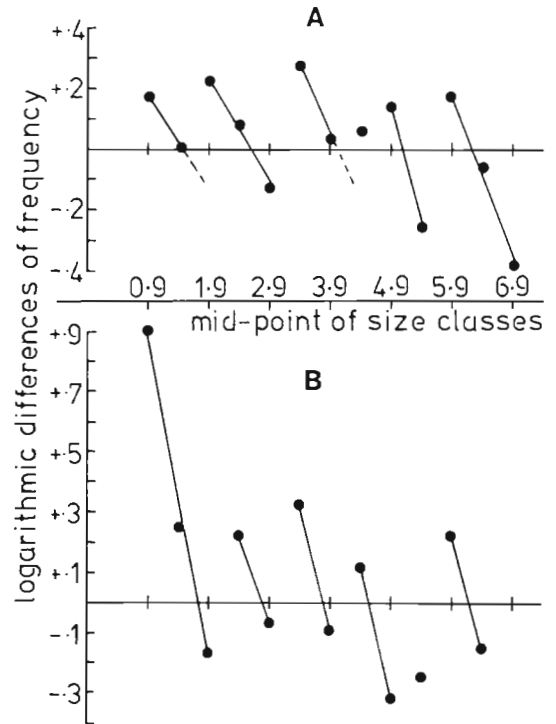


Fig. 1. *Mytilus edulis*. Size frequency analysis of shell lengths using the procedure of Bhattacharya (1967). In each sample 5 size classes are resolved. A: Lynher population; B: Cattewater population

Two growth models were then fitted to the presumed age-class data:

(1) The von Bertalanffy equation:

$$l_t = L_\infty [1 - e^{-k(t-t_0)}]$$

where l_t is length at time t , L_∞ a constant representing the asymptotic (or maximum) length, k a constant representing the rate at which the asymptotic length is approached, and t_0 a third constant representing time when $l_t = 0$.

(2) The Gompertz equation:

$$\log_{10} l_t = \log_{10} L_\infty [1 - e^{-k^1(t-t_1)}]$$

where k^1 is the rate constant and t_1 a constant representing time when $l_t = 1$.

Winsor (1932), Silliman (1968) and Hankioja and Hakala (1979) discuss the relative merits of these two growth models. The constants for each equation were derived as discussed by Theisen (1973) and Ricker (1975). Boetius (1962) and Theisen (1968) related the growth of *Mytilus edulis* to an integration of temperature and time called 'day-degrees' (D^0) and Ursin (1963) incorporated day-degrees as the independent variable in the Bertalanffy growth equation as:

$$l_D = L_\infty [1 - e^{-k_D(D-D^0)}]$$

where l_D is length at D day-degrees, k_D the rate con-

stant determined as k/D_y (D_y = annual sum of day-degrees), and $D_0 = t_0 \cdot D_y$. Day-degrees may also be incorporated into the Gompertz equation:

$$\log_{10} l_D = \log_{10} L_\infty [1 - e^{-k^1 D_y (D - D^1)}]$$

where D_1 is the day-degrees associated with t_1 . These equations were used to include monthly changes into the description of annual growth in length at the two sites.

Shell lengths were related to dry flesh weights (mantle, non-mantle and total) according to the allometric equation:

$$W = a \cdot L^b$$

Regression analyses on \log_{10} -transformed values of weight (W) and length (L) were carried out for each sample, followed by covariance analysis (Sokal and Rolf, 1969) to compare estimates of b and a .

Mature mussels may lose a large proportion of their body weight on spawning (Bayne, 1976; Griffiths, 1977; Griffiths and King, 1979; Thompson, 1979). Since a major proportion of the mature gonad develops within the mantle, weight losses from this tissue may be used as an estimate of fecundity. To be reliable, however, such estimates should be accompanied by histological evidence of the timing and duration of spawning and of the extent to which losses of gametes represent complete or only partial spawning. In this study, weight changes in the mantle were correlated with the results of a parallel histological study (Bayne and Widdows, 1978; Lowe et al., 1980) of gametogenesis in mussels from the two sites, and used to estimate the weight losses due to spawning.

Physiological measurements were made between May 1973 and May 1975 (Lynher) and October 1973 and March 1975 (Cattewater), as described by Bayne and Widdows (1978). In the present paper we introduce corrections for the production of pseudofaeces (i.e. material filtered from suspension but rejected by the mussel prior to ingestion) and we have adjusted our earlier values for absorption efficiency.

(1) *Pseudofaeces*. Widdows et al. (1979) estimated the seston (= total particulate matter in suspension) concentrations at which pseudofaeces production was initiated by *Mytilus edulis* of different sizes in the Lynher. We have calculated from these data, and from unpublished information from Widdows (pers. comm.), a relationship between the threshold concentration of seston above which ingestion rate does not increase with further increase in concentration of suspended particulate matter (T : mg l^{-1}) and the dry flesh weight of the mussel (W ; g):

$$T = 5.4W^{0.19} \quad (n = 5; r^2 = 0.72)$$

We assume the same relationship to hold for mussels

from both sites, which are similar in their total seston concentrations. The energy value of total seston was calculated from Widdows et al. (1979) and took seasonally variable values from 1.8 J mg^{-1} in the autumn and winter to 4.6 J mg^{-1} in the summer.

(2) *Absorption efficiency*. Bayne et al. (1979) recorded a relationship between absorption efficiency e and the proportion of organic matter (POM) present in the seston:

$$e = 0.5 \log_{10} O - 0.32 \quad (n = 26; r^2 = 0.76)$$

where O is (POM/Total seston) $\cdot 100$. We have used this relationship here, in favour of the values originally published by Bayne and Widdows (1978).

RESULTS

Analysis of Size Classes

The smallest size class, which was identifiable in the summer with a mode between 0.5 and 0.6 cm, was taken to represent mussels in their first summer after settlement (i.e. the I-year class) since these individuals were too large to have resulted from a larval settlement in the same year. Because these individuals were probably not sampled non-selectively, due to the mesh sizes used in sieving the samples, they were excluded from subsequent analysis. Larger sizes were assumed to represent successive age classes and their modal lengths calculated from each sample, to include year-classes II to VI. The means of these modal values, representing average annual shell lengths at each site, were as follows:

Year class	Lynher site	Cattewater site
II	1.33 cm	1.46 cm
III	2.87 cm	2.94 cm
IV	4.25 cm	3.99 cm
V	5.31 cm	4.77 cm
VI	6.06 cm	5.42 cm

Derivation of Growth Equations

Figure 2 shows a modified Ford Walford plot ($\log_{10} l_t$ vs $\log_{10} l_{t+1}$) constructed to estimate L_∞ and k^1 in the Gompertz equation for the Lynher site. The line of best fit was:

$$\log_{10} l_{t+1} = 0.537 \log_{10} l_t + 0.39$$

from which k^1 was calculated to be 0.584 and $\log_{10} L_\infty$ to be 0.838. Comparing the results of similar treat-

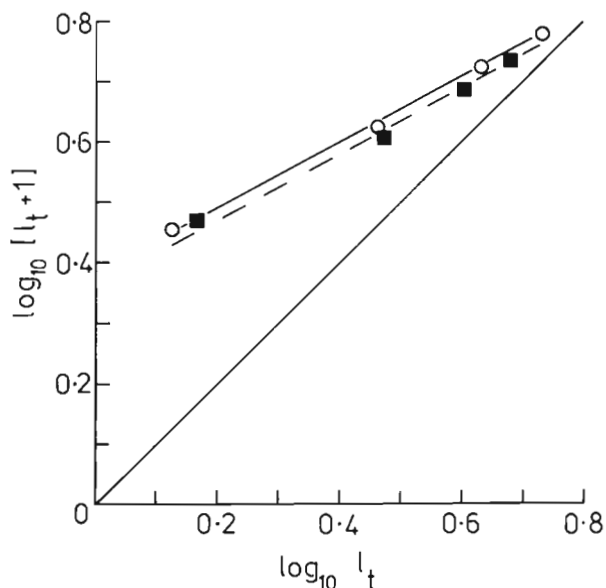


Fig. 2. *Mytilus edulis*. Modified Ford-Watford plot to estimate parameters for the Gompertz growth equation for two populations: circles: Lynher; squares: Cattewater

ments for both Bertalanffy and Gompertz equations for *Mytilus edulis* from both sites:

Fit		Lynher	Cattewater
Gompertz:	k^l	0.584	0.611
	L_∞	6.89 cm	6.35 cm
Bertalanffy:	k	0.222	0.237
	L_∞	9.38 cm	8.13 cm

Values for t_0 and t_1 were estimated by plotting

$$l_n \left[\frac{(L_\infty - l_t)}{l_t} \right]$$

(for the Bertalanffy fit) or

$$l_n \left[\frac{(\log_{10} L_\infty - \log_{10} l_t)}{\log_{10} l_t} \right]$$

(for the Gompertz fit) against time in years, fitting straight lines by least squares regression analysis, and solving for t_0 and t_1 , respectively. The results were:

Fit	Lynher	Cattewater
Gompertz (t_1):	1.77	1.50
Bertalanffy (t_0):	1.32	1.04

The relevant mean annual growth equations can now be written as:

- (1) Lynher Gompertz: $\log_{10} l_t = 0.838 [1 - e^{-0.584(t-1.77)}]$
 Bertalanffy: $l_t = 9.38 [1 - e^{-0.222(t-1.32)}]$
- (2) Cattewater Gompertz: $\log_{10} l_t = 0.803 [1 - e^{-0.611(t-1.50)}]$
 Bertalanffy: $l_t = 8.13 [1 - e^{-0.237(t-1.04)}]$

These equations are plotted in Figures 3 (Lynher site) and 4 (Cattewater site) together with modal year-class estimates, including those for year-class I. The data strongly suggest a sigmoidal growth form, so that

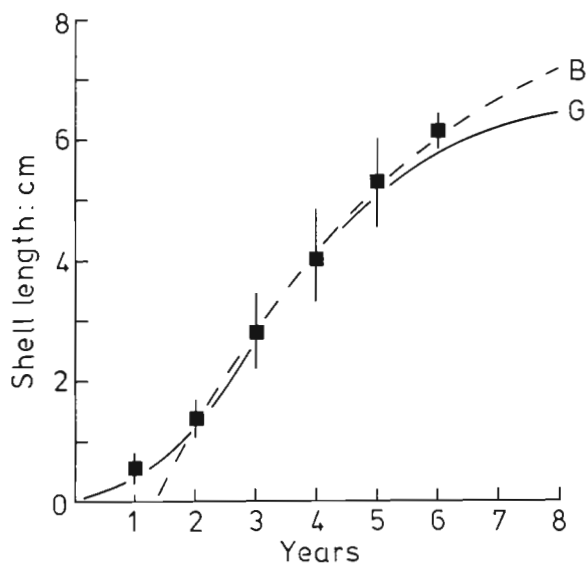


Fig. 3. *Mytilus edulis*. Von Bertalanffy (B) and Gompertz (G) growth curves for individuals from the Lynher site; squares: estimates (mean \pm SD) of modal shell lengths

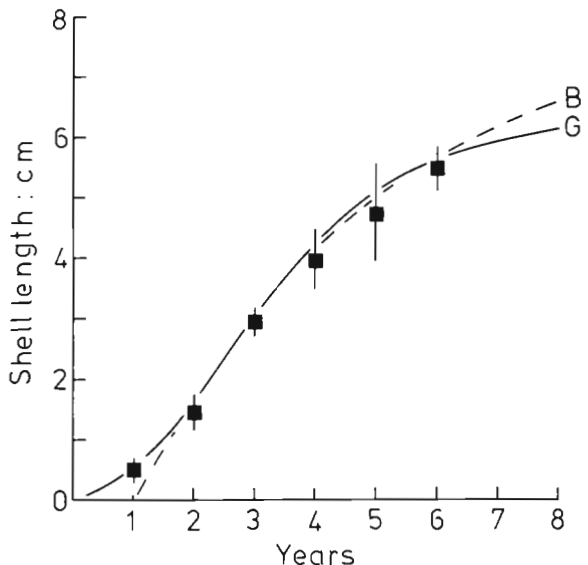


Fig. 4. *Mytilus edulis*. Von Bertalanffy (B) and Gompertz (G) growth curves for individuals from the Cattewater site; squares: estimates (mean \pm SD) of modal shell lengths

the Gompertz models provide the better fit. However, the Bertalanffy model provides an adequate fit to the data for the larger individuals and this equation possibly predicts more realistic asymptotic lengths. This is in good agreement with Theisen (1973). Both equations agree in suggesting a more rapid rate of growth for smaller individuals, and a smaller maximum length, at the Cattewater site.

An independent estimate of age for *Mytilus edulis* from the Lynher site was kindly made by R. A. Lutz (see Lutz, 1976; Lutz and Castagna, 1980, for procedure), who examined 6 specimens, 3 each of mean shell length 5.5 ± 0.2 cm and 6.7 ± 0.4 cm:

Age (years) (Lutz, pers. comm.)	Length (cm)		
	Lutz	Gompertz	Bertalanffy
5.5	5.5 ± 0.2	5.5	5.7
9.0	6.7 ± 0.4	6.7	7.7

Incorporation of Temperature into the Growth Equations

In the analysis that follows we treat only the Gompertz equations for each site. Monthly day-degrees (D° ; based on water temperature only) were higher at the Cattewater than the Lynher from November to May (Fig. 5); annual variation was greater at the Lynher.

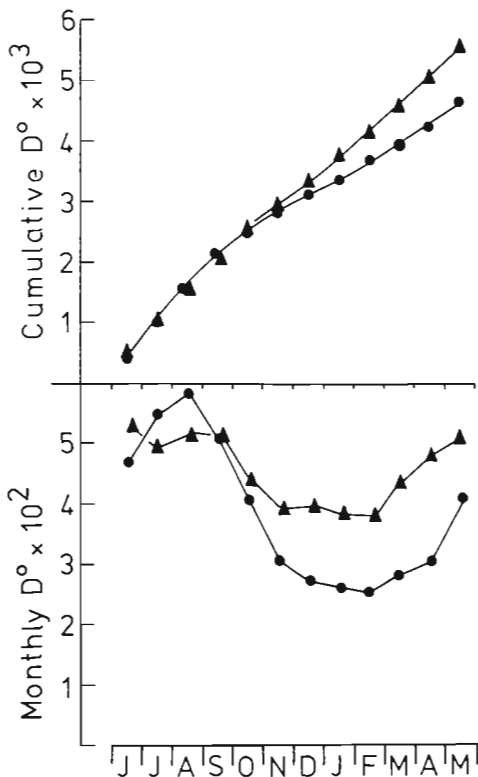


Fig. 5. *Mytilus edulis*. Monthly and cumulative day-degrees (D°) for two sites; circles: Lynher; triangles: Cattewater

Total annual day-degrees were: Lynher, 4620 D° ; Cattewater, 5550 D° . Incorporation into the Gompertz equations yielded:

Lynher: $\log_{10} l_D = 0.838 [1 - e^{-1.3 \times 10^{-4}(D - 8172)}]$
 Cattewater: $\log_{10} l_D = 0.803 [1 - e^{-1.7 \times 10^{-4}(D - 8323)}]$

In this treatment two assumptions are made: (1) that the value for L_∞ is independent of temperature, and (2) that the 'biological zero' for growth of *Mytilus edulis* occurs at 0 °C. The first of these assumptions is probably incorrect (Theisen, 1973) but is unlikely to be a serious constraint in these examples (Ursin, 1963). The second assumption is considered reasonable. The Gompertz equations with day-degrees were used to calculate monthly values for shell lengths for subsequent estimation of growth in weight from length/weight regressions.

Length/Weight Relationships

All regressions of dry flesh weight (W ; mg) and shell length (L ; mm) were highly significant and in no case was there a noteworthy difference between the results of functional and GM regression procedures (Ricker, 1975). For mussels from the Lynher site covariance analysis demonstrated no significant difference between estimates of slope (b) in the allometric relationship, and a common expression

$$W = a \cdot L^{2.83 \pm 0.11} \quad (n = 300; r^2 = 0.92)$$

was accepted, with seasonal variability in a . For the Cattewater site, however, covariance analysis indi-

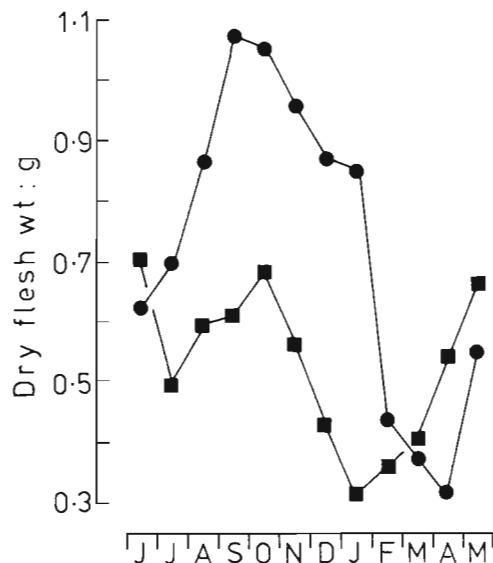


Fig. 6. *Mytilus edulis*. Dry flesh weights (g) of 6-cm shell length individuals in two populations, calculated from monthly length/weight regression analyses; squares: Lynher; circles: Cattewater

cated significant differences between estimates of b . The data were then grouped according to season and the following expressions derived:

Summer (June to August) : $W = a \cdot L^{2.70 \pm 0.11}$
 Autumn (September to November): $W = a \cdot L^{3.17 \pm 0.13}$
 Winter (December to February) : $W = a \cdot L^{3.31 \pm 0.09}$
 Spring (March to May) : $W = a \cdot L^{2.44 \pm 0.23}$

Seasonal changes in weight for individuals of 6 cm shell length from both populations are shown in Figure 6, demonstrating the large annual fluctuations in weight at both sites.

Energy Value

Regression analysis showed no significant change between energy value g^{-1} of tissue with change in dry flesh weight of the mussels between 0.1 and 1.0 g dry weight ($F = 0.14$ for 1, 105 degrees of freedom). Analysis of variance also demonstrated no significant difference between mussels from the two sites ($F = 3.09$ for 1, 10 d.f.). We have therefore taken a single overall mean value of $21.8 \pm 1.7 J mg^{-1}$ dry flesh weight as the energy value for *Mytilus edulis* tissue in this study. This is within the range normally found for marine bivalves (Beukema and De Bruin, 1979).

Growth in Weight

Data from the length/weight regressions were used to convert estimates of growth in length (from the Gompertz equations, calculated monthly against day degrees) to monthly estimates of growth in weight (Fig. 7). The strongly seasonal nature of growth at both sites

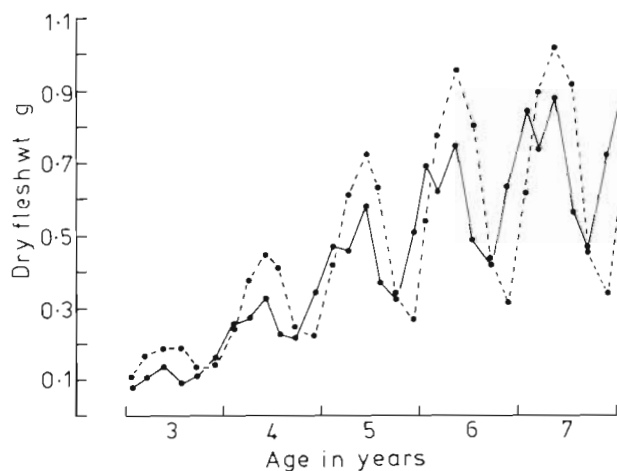


Fig. 7 *Mytilus edulis*. Growth in weight over 5 years in two populations; solid line: Lynher; broken line: Cattewater

is evident, with positive growth in the summer and negative growth in the winter. The amplitude of annual changes in weight was greater in mussels at the Cattewater and, particularly in the older year classes, the seasonal increase in weight was initiated earlier in the Lynher (February) than the Cattewater (April). Loss in weight by older mussels in the Lynher between June and August coincided with the first of two periods of spawning; a later spawning in October resulted in further loss of weight which was accentuated by the period of negative growth in the winter. At the Cattewater site there was no summer loss of weight (and no summer spawning); spawning occurred in September/October and was followed by a long period of negative growth (see also Fig. 6).

Fecundity

Covariance analysis of regressions relating mantle dry weight to shell length indicated a significant heterogeneity amongst slopes (b values) in the allometric equations at both sites. However, pooling the data according to season resulted in acceptable

Table 1. *Mytilus edulis*. Values for b and a (\pm S.D.) in the allometric equation relating dry weight of mantle tissue (W ; mg) to shell length (L ; cm) for two populations: $W = a \cdot L^b$

Population	Month/Year	$b \pm$ S.D.	$a \pm$ S.D.	
Lynher	June 1973	3.77 ± 0.38	$0.127 \pm .026$	
	July	3.77 ± 0.38	$0.146 \pm .095$	
	August	3.77 ± 0.38	$0.106 \pm .022$	
	September	4.40 ± 0.46	$0.060 \pm .010$	
	October	4.40 ± 0.46	$0.040 \pm .009$	
	November	4.40 ± 0.46	$0.025 \pm .004$	
	December	4.08 ± 0.40	$0.031 \pm .005$	
	January 1974	4.08 ± 0.40	$0.021 \pm .011$	
	March	4.84 ± 0.48	$0.010 \pm .001$	
	April	4.84 ± 0.48	$0.051 \pm .003$	
	June	3.77 ± 0.38	$0.139 \pm .045$	
	August	3.77 ± 0.38	$0.030 \pm .007$	
	Cattewater	September 1973	4.09 ± 0.45	$0.067 \pm .033$
		November	4.09 ± 0.45	$0.050 \pm .010$
January 1974		4.14 ± 0.32	$0.100 \pm .013$	
February		4.14 ± 0.32	$0.048 \pm .007$	
April		4.11 ± 0.30	$0.035 \pm .005$	
May		4.11 ± 0.30	$0.080 \pm .013$	
July		3.37 ± 0.32	$0.310 \pm .119$	
September		4.09 ± 0.45	$0.058 \pm .012$	
October		4.09 ± 0.45	$0.042 \pm .006$	

homogeneity, and intercept values (a) were adjusted accordingly (Table 1). Estimates of weight losses due to spawning were derived from the following regressions of mantle weight against shell length:

Lynher: July/August, 1973;
 September/October, 1973;
 June/August, 1974
 Cattewater: September/November, 1973;
 September/October, 1974

The calculated spawning losses (W^* ; mg) were then related to the total body weights (W ; g) before spawning and two equations from the pooled data derived:

Lynher: $W^* = 104 \pm 23.W^{1.40 \pm 0.13}$ ($n = 18, r^2 = 0.93$)

Cattewater: $W^* = 21 \pm 2.W^{1.29 \pm 0.09}$ ($n = 12, r^2 = 0.91$)

The slopes of these two relationships are similar; at similar body weights, however, the weight losses which were taken to represent fecundity were greater in *Mytilus edulis* from the Lynher. In addition, mussels at the Lynher site spawned twice during the year, compared with a single spawning in the Cattewater (Lowe et al., 1980).

Physiological Estimation of Growth

Pseudofaeces Production

Above a certain concentration of particulate matter in suspension, the ingestion rate of *Mytilus edulis* is held constant by the production of pseudofaeces (Widdows et al., 1979), up to a very high seston concentration (> 150 mg⁻¹) above which both clearance rate (litres of water cleared of seston by the individual mussel) and pseudofaeces production decline. The relationships between the production of pseudofaeces, the seston concentration and the size of the mussel are complex. (Foster-Smith, 1975; Widdows et al., 1979). Using the expression for the threshold concentration of seston quoted earlier ($T = 5.4W^{0.19}$), we have calculated the proportion of material cleared from suspension that is subsequently rejected as pseudofaeces by a mussel weighing 0.5 g dry weight of flesh (Fig. 8) for comparison with values taken from Foster-Smith (1975) for a similarly sized mussel feeding on a suspension of *Phaeodactylum* cells. The form of the two curves is similar. However, the mussels feeding on natural particulates show a higher threshold concentration for pseudofaeces production.

In the present study, when measured clearance rates were multiplied by observed seston concentrations (data from Bayne and Widdows, 1978), the values all exceeded the threshold for maximum ingestion rate, T , signifying the production of pseudofaeces by mussels at both sites. We have therefore calculated ingestion rate (Jh^{-1}) as the weight-corrected value for T multiplied by clearance rate and converted to energy units

using the seasonally variable energy value for total seston.

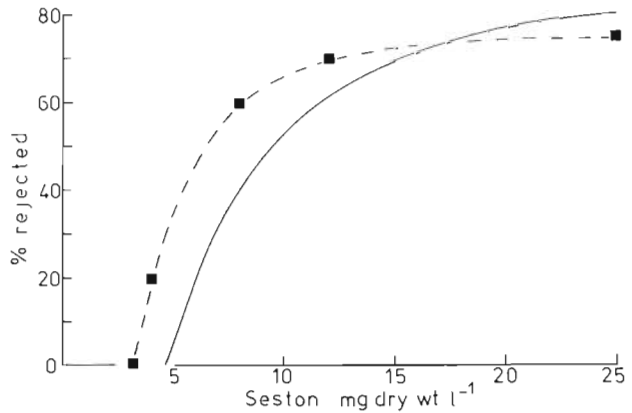


Fig. 8. *Mytilus edulis*. Proportion of particulate material cleared from suspension rejected as pseudofaeces (individuals of 0.6 g dry tissue weight) as a function of seston concentration (mg dry weight l⁻¹); squares: values calculated from Foster-Smith (1975); solid line: relationship derived from the equation (see text) for the threshold concentration for maximal ingestion rate

Absorption Efficiency

Figure 9 compares calculated and observed values for absorption efficiency at both sites; differences were slight for most months of the year.

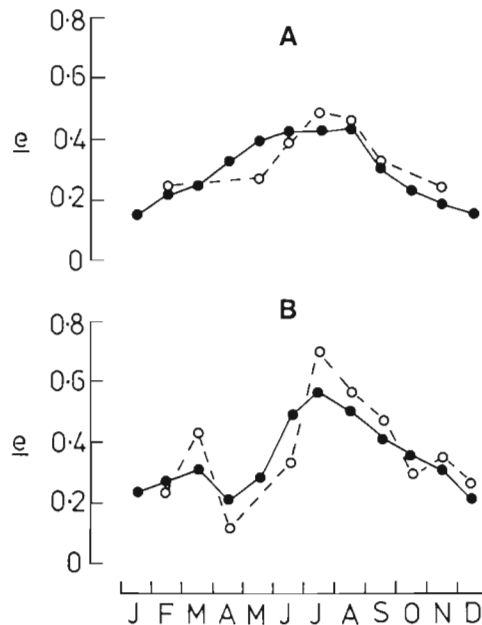


Fig. 9. *Mytilus edulis*. Comparison of calculated and observed absorption efficiencies (e) in two populations. Open circles: observed (Bayne and Widdows, 1978); closed circles: calculated (see text and Bayne et al., 1979). A: Lynher population; B: Cattewater population

The Scope for Growth

This was calculated from the energy balance equation of Winberg (1960);

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

where C = ingested ration

P = production, both somatic (Pg) and germinal (Pr)

R = respiratory heat loss

U = energy lost as excreta

F = energy lost as faeces

The absorbed ration, A, is $C \times e$, where e is the efficiency of absorption. Production (Pr + Pg) can then be expressed as a function of A, R and U:

$$P = A - (R + U),$$

and is called the 'scope for growth'.

The scope for growth of an individual *Mytilus edulis* from each site was calculated in monthly increments, starting with an individual of 100 mg dry flesh weight on 1 June of the third summer after settlement. Mussels from the Lynher site were assumed to spawn in June and September, those from the Cattewater in September only. The results of simulated growth over 5 years are plotted in Figures 10 and 11 together with growth estimates using the Gompertz equations.

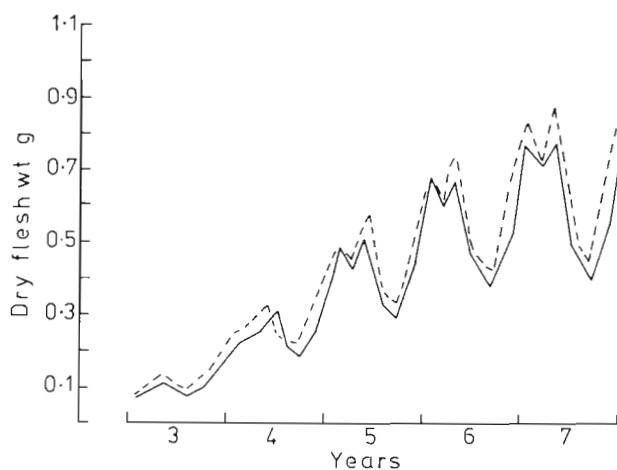


Fig. 10. *Mytilus edulis*. Comparison of growth in weight (Lynher site) as calculated from age-class analysis (broken line) and from physiological estimates of the scope for growth (solid line)

The main features of the two growth curves are similar for mussels at each site *viz.* periods of negative growth in the winter and positive growth in the summer and autumn. There is reasonable agreement also in the mean weights predicted for each age class, although maximum annual weights are somewhat overestimated at the Cattewater site by the physiological derivation. The growth curves agree in predicting an earlier recovery to positive growth in the Lynher

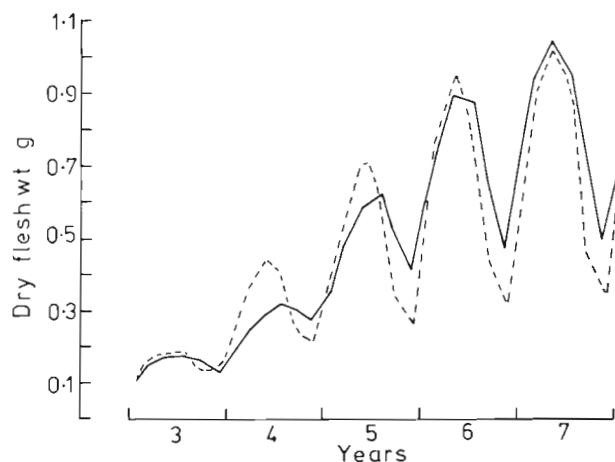


Fig. 11. *Mytilus edulis*. Comparison of growth in weight (Cattewater site) as calculated from age-class analysis (broken line) and from physiological estimates of the scope for growth (solid line)

than in the Cattewater, and a greater amplitude to the annual growth pattern at the latter site.

DISCUSSION

Annual rates of growth in length were similar in *Mytilus edulis* at the two sites studied, with individuals taking approximately 5 years from settlement to grow to 5 cm shell length. However, when differences in ambient water temperatures were taken into account, by incorporating time and temperature as day-degrees, the rates of growth in the Cattewater were seen to be less than in the Lynher, in spite of higher temperatures at the former site. This was unexpected since, in general, rates of growth of marine invertebrates increase with rise in temperature over the ecological range of the species (e.g. Newell, 1979). The higher temperatures in the Cattewater occurred in the winter and spring and the implication is that this unseasonable rise in temperature at a time of poor food quality (Bayne and Widdows, 1978) caused a reduction in the rate of growth.

The rates of growth in length at both sites were low compared with many published values for marine mussels, although they were of the same order as some other littoral populations (Seed, 1976). In the more recent literature, Griffiths and King (1979), Griffiths (1980) and Wallace (1980) have recorded *Aulacomya ater*, *Choromytilus meridionalis* (both from South Africa) and *Mytilus edulis* (from Norway), respectively, as requiring 5 to 6 years to grow to 5 cm length. Growth in other situations may be much more rapid, with individuals reaching 5 cm in less than 18 months; e.g. *Perna perna* in South Africa and New Zealand (Berry,

1978; Hickman, 1979), *C. meridionalis* on the west coast of South Africa (Du Plessis, 1977) and *M. edulis* in suspended cultivation in Spain (Mason, 1976). Rates of growth of *M. edulis* in North America have recently been compiled by Lutz (1980); they vary over the range indicated here i.e. 5 cm shell length reached from <2 to > 6 years. Some of this variation in growth rate can be explained by temperature differences, as demonstrated by calculating growth in length (mm) per 1000 D° (although non-linear relationships between age, rate of growth and D° make comparative use of such data difficult). Hickman (1979) made this calculation from various studies of mussels grown in suspended culture (values ranged from 8.9 to 15.2 mm per 1000 D°); some values for littoral populations are listed in Table 2, but with no corrections made for height on the

Table 2. *Mytilus edulis*. Rates of growth expressed as mm increase in shell length per 1000 day degrees, from various locations. + Calculated by Theisen, 1968

Location	Rate of growth (mm per 1000 D°)	Authority
Conway; North Wales	3.3	Savage (1956) +
Oresund; Denmark	7.0	Boetius (1962)
Wadden Sea; Denmark	8.3	Theisen (1968)
Disko; Greenland	5.5	Theisen (1973)
Menai Straits; North Wales	4.5	Dare and Edwards (1976)
Lynher; Cornwall, U.K.	3.2	This study
Cattewater; Devon, U.K.	3.2	This study

shore (Baird, 1966). Remaining differences in growth rate may still be considerable.

Mussels from the Cattewater site had lower values for annual growth in weight than those from the Lynher, but with a greater amplitude in weight in any single year. There were differences also at the two sites in the timing and the duration of the annual periods of weight increase and decrease, and in fecundity. Fecundity in both populations was somewhat lower than other published values for *Mytilus edulis* (Table 3). Values in Table 3 were calculated from Thompson (1979); the slopes in the expressions relating weight loss on spawning to body weight are all greater than one (range 1.12–1.51) and the weight loss (in mg) for an individual of 1 g dry flesh weight ranges from 21 to 471 mg. Thompson recorded annual variation in fecundity within populations of mussels; there are also considerable between-population differences. In a study of mussels from the vicinity of a thermal discharge Hines (1979) recorded reduced gonad indices and body con-

Table 3. *Mytilus edulis*. Equations describing dry weight loss on spawning (W^* , in mg; calculated from changes in mantle dry weight) as related to total dry body weight before spawning (W , in g) for different populations

Population	Allometric equation	Authority
Bellevue:	max. $W^* = 398.W^{1.124}$ min. $W^* = 294.W^{1.124}$	Thompson (1979) Thompson (1979)
Long Island:	$W^* = 308.W^{1.269}$	Thompson (1979)
Petpeswick:	max. $W^* = 471.W^{1.481}$ min. $W^* = 277.W^{1.481}$	Thompson (1979) Thompson (1979)
Lynher:	$W^* = 104.W^{1.40}$	This study
Cattewater:	$W^* = 21.W^{1.29}$	This study
Mothecombe:	$W^* = 193.W^{1.51}$	Worrall (unpubl.)

dition indices which he ascribed to stressful temperatures, a conclusion similar to our own.

The good agreement between estimates of growth by size-class discrimination and by physiological measurements suggests that some of the features of the seasonal patterns of growth might be explained by a closer analysis of the physiological data. Bayne and Widdows (1978) demonstrated a correlation between rates of oxygen consumption and the seasonal gametogenic cycle in *Mytilus edulis* from the Lynher and Cattewater sites; no significant correlations emerged between oxygen uptake and temperature or the concentration of particulate organic matter. The rate of clearance of particles from suspension was negatively correlated with the concentration of total seston.

In taking these analyses further, correlation coefficients were calculated between monthly growth rates ($\ln W_2 - \ln W_1$, from the size class analysis) and either (a) the ratio of particulates cleared from suspension (in Joules) to the sum of energy losses due to respiration and excretion, or (b) the ratio of absorbed ration to the summed energy losses. For mussels at the Lynher site the first correlation was not statistically significant ($r^2 = 0.31$; 10 d.f., $P > 0.05$) whereas the second correlation was highly significant ($r^2 = 0.94$; $P < 0.001$). For mussels from the Cattewater both correlations were significant ($r^2 = 0.69$ and 0.81 , respectively). At both sites the concentrations of seston exceeded the threshold concentrations for pseudofaeces production, so that the amount of material ingested remained at a maximum throughout the year. However, the proportion of this seston composed of organic matter was highly variable with season and much more so in the Lynher (variance : mean ratio = 540 %) than in the Cattewater (290 %).

These results emphasise the importance of the ration in affecting the seasonal growth pattern, although it is not the total seston available, nor even the total

amount of particulate organic matter, but the proportion between these two variables which was significant. The efficiency with which the individual mussels absorbed useful energy from material ingested, rather than the rate of feeding *per se*, controlled the supply of energy, and this efficiency (e), as well as the total amount of available energy, were both a function of the proportion of organic matter in the ingested seston. At the Cattewater site, total seston and the proportion of organic matter co-varied during the year, but this was not so in the Lynher (see also Widdows et al., 1979), resulting in a lack of significant correlation between the amount of material cleared from suspension and growth at the latter site.

Another major seasonal cycle in these mussels was that of gametogenesis and spawning. Two features distinguished mussels from the two sites *viz.* two spawnings per year in the Lynher compared with one only (in the autumn) in the Cattewater, and a higher fecundity per spawning in the Lynher. For mussels in the Lynher the loss of weight in the winter (46 %) was less than in the Cattewater (67 %) and the period of weight gain in the spring started earlier. Experimental work with bivalves (Sastry, 1968, 1970; Gimazane, 1972; Bayne, 1975) demonstrates that gametogenesis may be initiated by a rise in temperature only if sufficient nutrient reserves within the animal, or food in the environment, are present. Stressful temperatures in the winter and spring in the Cattewater, together with poor ration conditions, possibly inhibit gametogenesis following the spawning in the autumn, whereas in the Lynher, gametogenesis can be maintained in the winter and spring, resulting in a spawning in the summer. This pattern for the Lynher appears typical of many mussel populations (Gabbott, 1976; Bayne, 1976; Lowe et al., 1980). Temperature and ration conditions during the summer were suitable at

both sites for sufficient gametogenesis to occur for an autumn spawning, although with a lower fecundity in the Cattewater.

The seasonal changes in body weight, including those due to spawning, result in very variable turnover ratios ($P\bar{W}^{-1}$, where P is production of both somatic tissues and gametes, and \bar{W} is the mean body weight or energy content) during the year. For example, for individuals in year class IV, monthly $P\bar{W}^{-1}$ varied from -0.34 to $+0.42$ in the Lynher and -0.59 to $+0.66$ in the Cattewater. When calculated annually (Table 4), *Mytilus edulis* from the Lynher are seen to have been more productive, with higher turnover ratios and a greater proportion of energy directed towards reproduction (Pr) than mussels in the Cattewater.

Bearing in mind the known temperature differences at the two sites, the $P\bar{W}$ ratios from Table 4 were plotted against cumulative day degrees (Fig. 12). The result demonstrates that somatic production per unit body weight ($Pg\bar{W}^{-1}$) was similar at both sites when temperature differences were taken into account, but that gamete production per unit body weight ($Pr\bar{W}^{-1}$) was considerably less in the Cattewater. Previous experimental work in this laboratory has demonstrated reduced fecundity in mussels exposed to temperature and nutritive stress (Bayne et al., 1978); the present results suggest a similar phenomenon occurring naturally in the Cattewater.

This study illustrates the mutual advantages of growth estimates and physiological studies in exploring difference in the production potential by individuals of the same species at different sites. The growth estimates identified difference in overall growth rates and in the details of the seasonal cycle. The physiological studies (see also Bayne and Widdows, 1978) suggest a number of factors likely to cause the observed growth differences; perhaps the most striking of these

Table 4. *Mytilus edulis*. Mean individual biomass (\bar{W} ; body energy content in June), production (P = total production; Pg = somatic production; Pr = gamete production), turnover ratios (P/\bar{W}) and reproductive effort ($Pr/P \cdot 100$) for individuals from two sites in southern England

Location	Years of settlement	\bar{W} (kJ)	P (kJ y^{-1})	Pg (kJ y^{-1})	Pr (kJ y^{-1})	P/\bar{W}	$\left[\frac{Pr}{P}\right] \cdot 100$
Lynher	3-4	1.92	4.52	4.30	0.22	2.35	4.8
	4-5	6.22	6.39	5.56	0.83	1.03	12.9
	5-6	11.78	6.76	5.01	1.75	0.57	25.9
	6-7	16.79	6.22	3.57	2.65	0.37	42.6
	7-8	20.36	5.54	2.21	3.33	0.27	60.1
Cattewater	3-4	2.74	3.72	3.67	0.05	1.35	1.3
	4-5	6.41	3.86	3.74	0.12	0.60	3.1
	5-6	10.16	3.11	2.87	0.24	0.31	7.8
	6-7	13.02	2.23	1.89	0.34	0.17	15.2
	7-8	14.92	1.48	1.09	0.39	0.10	26.2

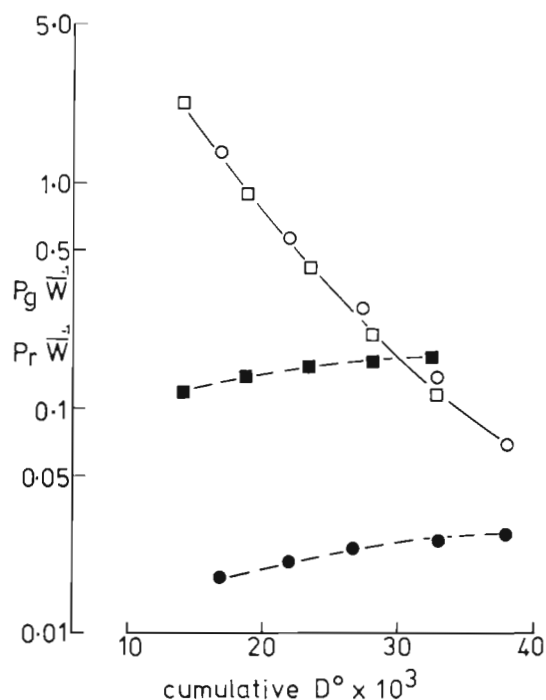


Fig. 12. *Mytilus edulis*. Turnover ratios for somatic production ($P_g \bar{W}^{-1}$; open squares, open circles) and for gamete production ($P_r \bar{W}^{-1}$; closed squares, closed circles) for individuals from Lynher (squares) and Cattewater (circles) sites

is variable absorption efficiencies, which reflect differences in the quality of the physiologically available ration at the two sites. The temperature differences that also characterise the two sites, coupled with differences in ration, have a major effect on the fecundity of the mussels. When these studies are linked with estimates of mortality and recruitment (Freeman and Dickie, 1979; Bayne and Worrall, unpublished) a comprehensive understanding of production differences becomes possible.

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