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Reproductive effort and value in different populations of the marine mussel, *Mytilus edulis* L.

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Summary. Fecundity, reproductive effort (estimated both from production measurements and from physiological data), the energetic costs of reproduction and the reproductive value of different size classes were measured for mussels at different sites and related to age and to tissue weight. Variability between sites was considerable and differences as great as 10 × were recorded between minimum and maximum values for egg production, reproductive effort and reproductive value. However, similarities between mussels from different sites were also apparent, as regards egg size, the estimated metabolic costs of egg production (based on measurements of oxygen consumption), the relationship (isometric) between egg production and body size, the fact of an increase in reproductive effort with increase in size, and the age at which maximum residual reproductive values was expressed. These relationships are discussed in terms of the fundamental reproductive strategy of the species and the degree of environmental stress imposed on the mussels at the different sites.

Introduction

The mussel, in common with many other marine lamellibranch molluscs, reproduces by means of gametes released into the water, where fertilisation takes place. There follows a period of planktotrophic larval development which terminates with settlement (and metamorphosis) onto benthic substrates. This type of reproduction is correlated (Sastry 1980; Calow 1983) with the production of a large number ($>10^4$) of small (<100 μm diameter) eggs. In addition, the mussel is iteroparous, reproducing annually (and occasionally more frequently) whilst continuing to grow. The reproductive cycle, annual or otherwise, is associated with an energy storage cycle (Gabbott 1976; 1983) which usually comprises the synthesis of carbohydrate and lipid reserves during periods of nutrient surplus, followed by the utilisation of these reserves for both somatic maintenance and gametogenesis during periods of relative nutrient scarcity.

The proportion of an organism's energy budget that is allocated to reproduction is termed the reproductive effort although, in practice, various methods to measure reproductive effort have been proposed (Fisher 1930; Williams 1966; Hirshfield and Tinkle 1975; Calow 1979, 1983). Reproductive effort by iteroparous molluscs, however measured, tends to increase with size and age. Browne and Russell-Hunter (1978) and Calow (1983) have reviewed such measurements; recent studies of individual species and/or genera include Faller-Fritsch (1977), Hughes and Roberts (1980) and Hart and Begon (1982), all on species of *Littorina*; Todd (1979) on nudibranchs; Parry (1982; see also Branch, 1982), on limpets; Perron (1982) on *Conus* spp; Aldridge (1982) on the freshwater snail *Leptoxis*; and studies on various bivalve species by Lucas et al. (1978), Griffiths and King (1979), Thompson (1979), Griffiths (1981), Shafee and Lucas (1980), Bayne and Worrall (1980) and Vahl (1982).

In general, reproductive effort rises asymptotically over the adult life span of planktotrophic, iteroparous bivalves. For example, when measured as the proportion of non-respired absorbed energy allocated to reproduction, there is an increase from zero to 100% over one to twelve years in *Mytilus edulis* (Bayne 1976; Thompson 1979). Bayne and Worrall (1980) recorded an age-related increase in reproductive effort in this species and also observed an increase in reproductive production (*Pr*; see Material and methods) per unit body weight (i.e. $Pr \cdot W^{-1}$). In other words, with an increase in body size an increasing proportion of body calories is allocated to reproduction. The high fecundity of this animal is therefore associated with increased energetic risks as the individuals age (Perron 1982; Vahl 1982).

A considerable body of theory has developed which explores the evolutionary implications and the adaptive significance of various reproductive "tactics" of this kind (see Stearns 1976, 1980). However, the extent and the significance of intraspecific variability in reproductive pattern have not been considered to the same extent. A species presumably has an evolved suite of life-history traits which may then be varied, within the basic pattern, in response to environmental changes (Hart and Begon 1982). This phenotypic variability must be considered in any assessment of the adaptive value of particular reproductive behaviour (Goodman 1979). In physiological terms, variability of reproductive pattern can be assessed as the differential allocation of resources to reproduction, and the energetic costs associated with such responses.

This paper reports measurements of reproductive effort by individual mussels from different sites and different types of environment. Reproductive effort is related to energetic costs and to measures of reproductive value which, as de-

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fined below (see Fisher 1930; Williams 1966), is a measure of the value to the population of a particular reproductive and growth pattern.

Material and methods

Mussels were studied at six sites on the English and Welsh coasts (Table 1). At all of these sites except Kings Dock, Swansea, where the mussels were sub-tidal, individuals were collected from mean low water mark of neap tides. In other respects the sites represented quite different habitats for the species, as indicated in Table 1.

The fecundity of individual mussels was measured both directly and indirectly. For direct measurements, mussels were induced to spawn in the laboratory by injection with 0.5 m KCl followed by exposure to an increase in temperature; the eggs released were counted by Coulter Counter and egg weights measured after rinsing on preweighed glass-fibre filters with isotonic ammonium formate and then drying for 24 h at 90° C. Indirect determinations were based on mean flesh weights before and after spawning was known (by histological inspection) to have occurred i.e. as the "weight loss on spawning" (Thompson 1979; Bayne and Worrall 1980).

Physiological measurements were made on individuals from most of the sites. These measurements were carried out in the field, under ambient conditions, using a mobile laboratory, and based on methods described by Bayne et al. (1977) and Bayne and Widdows (1978); they included rates of oxygen consumption, rates of feeding and absorption efficiency. The results of these determinations were used, together with measurements of the available ration, to estimate the energy available for growth and reproduction i.e. the "scope for growth" (Bayne and Widdows 1978). The food available to mussels at each site was determined by collecting suspended particulate material on pre-weighed glass-fibre filters, and analysing for particulate organic matter and for protein, carbohydrate and lipid content following methods described by Widdows et al. (1979). The statistical analysis of the results was based on standard procedures, including least squares regression and co-variance analyses.

Two indices of reproductive effort are used. Both depend on the evaluation of the energy equation:

$$P=P_r+P_g=C\cdot e-R \tag{1}$$

where
P = total production,
P_r = production of gametes,
P_g = production of somatic tissue,
C = the ingested ration,
e = absorption efficiency, and
R = energy lost via respiration,
all calculated in energy units. For some aspects of the study P was determined from estimates of age-related changes in weight (to derive P_g) and measured weight losses due to spawning (P_r). Reproductive effort is then

$$\text{Effort}=[P_r/(P_r+P_g)]\cdot 100. \tag{2}$$

In other cases, P was estimated physiologically, in which case

$$\text{Effort}=[P_r/(C\cdot e-R)]\cdot 100. \tag{3}$$

Calow (1979) proposed an index of the costs of reproduction, based on the energy allocation to reproduction (P_r) evaluated with respect to the metabolic demands of the maintenance of somatic tissue (R^*):

$$C=1-\left[\frac{C\cdot e-P_r}{R^*}\right]. \tag{4}$$

If the difference between the total energy loss through respiration (R) and the maintenance demand (R^*) is taken to represent the energy demands of reproduction (but including other activities) an alternative to this index of cost may be written:

$$C=1-\left[\frac{(C\cdot e)-(P_r+R-R^*)}{R^*}\right]. \tag{5}$$

Both of these indices require the estimation of R^*, which is difficult from field data on oxygen consumption. One method for estimating R^* is described in the Results sec-

Table 1. Notes to describe the local habitat of mussels at six sites in England and Wales

Site	Brief description of environmental conditions
Lynher; S.W. England (Tamar estuary system)	Estuarine site. Temperatures normal for temperate, inshore waters; salinity range 12–33$^0/_{00}$; seston concentrations variable < 5 to > 20 mg·l^{-1}. Extensive, well-established population.
Cattewater; S.W. England (Plym estuary, mouth)	Adjacent to cooling-water outfall of an electricity-generating station. Temperatures very variable (seasonally 11–19° C), abnormally high in the winter; salinity range 28–34$^0/_{00}$; seston concentrations high and variable. (See Bayne and Widdows, 1978)
Mothecombe (Erme estuary, mouth)	Estuarine site. Temperatures normal for temperate, inshore waters; salinity variable; seston concentrations high, with low organic content. Substrate coarse sand and gravel; scattered population.
Kings Dock; Swansea (South Wales)	Sub-littoral population. Temperatures and salinities normal for temperate, inshore sites; low seston loads (5 mg l^{-1}), high in organic content. Site subjected to shipping movements, low, chronic industrial pollution, summer thermal stratification.
Mumbles; South Wales (Bristol Channel)	Exposed coastal site. Temperatures and salinities normal for temperate, inshore sites; high seston loads with low organic content. Coarse gravel substrate, close by sewage outfall. Somewhat scattered population, subject to wave exposure and rapid tidal currents.
Swale; E. England (Thames estuary, mouth)	Coastal site (minimal estuarine influence). Normal temperate, inshore temperatures and salinities; high seston concentrations with variable organic content due to local pulp mill effluent. Scattered population.

tion; the energetic costs of reproduction[1] were then assessed using Eq. (5).

Residual reproductive value is a measure of the survival probability and the future fecundity of parents. Fisher (1930) first formulated the concept of reproductive value to include the average number of young that a female is expected to produce over her entire adult life. Williams (1966) partitioned lifetime reproductive value into one term (m_x) describing immediate reproductive potential (current fecundity) and a second term, called the residual reproductive value or RRV, which represents future reproductive potential (Pianka 1978). Total reproductive value for a stable population is then

$$V_x = m_x + \sum_{t=x+1}^{\omega} \frac{l_{t \cdot m_t}}{l_x} \tag{6}$$

where l_t/l_x represents the probability of survival from age x to age t; m_t is the average fecundity at age t; and ω is the age of last reproduction.

Residual reproductive value was calculated from data on mortality and expected fecundity. Mortality rates were determined from observed size- and frequency-distributions within the populations, using the method I described by Van Sickle (1977). This method requires information, not only on the size-distribution, but also on the growth of individuals at each site. The Bertalanffy equations fitted by Bayne and Worrall (1980) for mussels from the Lynher and Cattewater sites were used for this purpose and the following equation fitted, in a similar manner, to individuals from Mothecombe:

$$L_t = 8.50\,[l - e^{-0.284\,(t-1.53)}].$$

The assumption that these mussel populations were in steady-state with respect to year-class strengths is believed to hold (over a three-year period) for the Lynher site (unpublished data) but has not been tested for the other sites considered.

Results

1. Fecundity

Direct estimates. The mean dry weights of eggs spawned by ten females from four sites (Lynher: 10^6 eggs weighed 33.9 ± 7.5 (SD) mg. Kings Dock: 30.9 ± 7.5 mg. Swale: 34.9 ± 9.0 mg. Mumbles: 45.7 ± 18.3 mg) did not differ significantly when analysed for variance between and within samples ($F = 2.49$ for 3, 36 d.f; $P > 0.05$). An overall mean value was therefore calculated for $n = 40$ females:

Mean dry wt 10^6 eggs $= 36.2 \pm 11.6$ mg.

This value was used to convert counts of numbers of eggs spawned per female to an estimate of weight (Table 2). The size range of adults successfully induced to spawn from the Lynher and Kings Dock sites allowed the fitting of regression equations relating fecundity to the post-spawned dry flesh weights of the females. Weight-specific fecundity was highest in the Swale and lowest at Mumbles.

Indirect estimates. Equations for weight loss on spawning for mussels from two sites (1973/74) were presented by Bayne and Worrall (1980):

Lynher $W^* = 208\ (\pm 37) \cdot W^{1.40(\pm 0.13)}$

Cattewater $W^* = 21(\pm 2) \cdot W^{1.29(\pm 0.09)}$

Where W^* is annual weight loss in mg (encompassing two spawnings per year in the Lynher; Lowe et al. 1982) and W is dry flesh weight before spawning (in grams). Similar estimates were made for three other sites (Table 3). Spawning weight losses were greatest at Mothecombe, least in the Cattewater, with a difference between these sites of approx. 10 ×.

Comparisons between direct and indirect estimates of fecundity. This comparison is possible for three sites. For a female of 0.6 gram dry flesh weight, spawning weight losses (in mg) were:

	Direct method	Indirect method
Lynher	37.9 ± 2.5	37.8 ± 8.3
Kings Dock	26.5 ± 6.7	34.2 ± 3.5
Swale	62.0 ± 21.1	73.2 ± 18.6

(The quoted standard deviations are based on variance: mean ratios in the original data). The comparisons suggest no significant differences in the results of the two methods.

Comparisons of exponents relating spawning weight losses to body weight are possible for two sites:

Lynher: 1.40 ± 0.13 and 1.02 ± 0.21,
Kings Dock: 1.07 ± 0.12 and 1.15 ± 0.18.

The results do not support the adoption of an exponent greater than 1.0 and in calculations that follow it is assumed

Table 2. The fecundity of female *M. edulis* from four sites, expressed as numbers of eggs released per spawning and as the weight of eggs spawned, the latter based on a mean dry weight of 10^6 eggs of 36.2 mg (see text). Results for Lynher and Kings Dock are quoted as regression equations against the dry flesh weight (post-spawned) of the adult (W; in grams). Values are quoted ±S.D.

Site	Numbers of individuals spawned	Tissue dry wts of adults after spawning (g)	Numbers of eggs spawned	Weight of eggs spawned (mg dry)
Lynher	18	Range: 0.41–2.52	$1.66\ (\pm 0.11) \cdot 10^6 \cdot W^{1.02\ (\pm 0.21)}$	$60 \cdot W^{1.02}$
Kings Dock	20	Range: 0.59 ± 3.90	$1.26\ (\pm 0.32) \cdot 10^6 \cdot \mathrm{W}^{1.15\ (\pm 0.18)}$	$46 \cdot W^{1.15}$
Swale	10	0.61 ± 0.16	$1.91\ (\pm 0.65) \cdot 10^6$	113[a]
Mumbles	15	0.59 ± 0.15	$0.57\ (\pm 0.36) \cdot 10^6$	35[a]

[a] These values are "corrected" to a body size of 1 gram dry flesh weight (for comparison) assuming an isometric relationship (see text) between fecundity and body weight

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[1] The "energetic" costs of reproduction are not to be confused with the "adaptive" costs, which are defined by Hirshfield and Tinkle (1975) as "the difference between residual reproductive value when effort is zero and that residual reproductive value accompanying that particular expenditure of effort" (p. 2218)

Table 3. The fecundity of female *M. edulis* from five sites, estimated as the weight loss per spawning (W^*; mg) and related to the dry flesh weight of the adults before spawning (W; g). Results are "indirect" determinations of fecundity (see text)

Site	Numbers of individuals considered	Equations describing weight loss on spawning: 1) As fitted to original data	2) As re-fitted using an exponent = 1.0
Kings Dock	18	$W^* = 59\,(\pm\ 6)\cdot W^{1.07\,(\pm 0.12)}$	$W^* = 57\cdot W$
Swale	17	$= 156\,(\pm 26)\cdot W^{1.27\,(\pm 0.15)}$	$= 122\cdot W$
Mothecombe	20	$= 193\,(\pm 32)\cdot W^{1.21\,(\pm 0.23)}$	$= 179\cdot W$
Lynher[a]	18	$= 104\,(\pm 23)\cdot W^{1.40\,(\pm 0.13)}$	$= 63\cdot W$
Cattewater[a]	12	$= 21\,(\pm\ 2)\cdot W^{1.29\,(\pm 0.09)}$	$= 19\cdot W$

[a] Date for Lynher and Cattewater from Bayne and Worrall (1980). Values are quoted ± S.D.

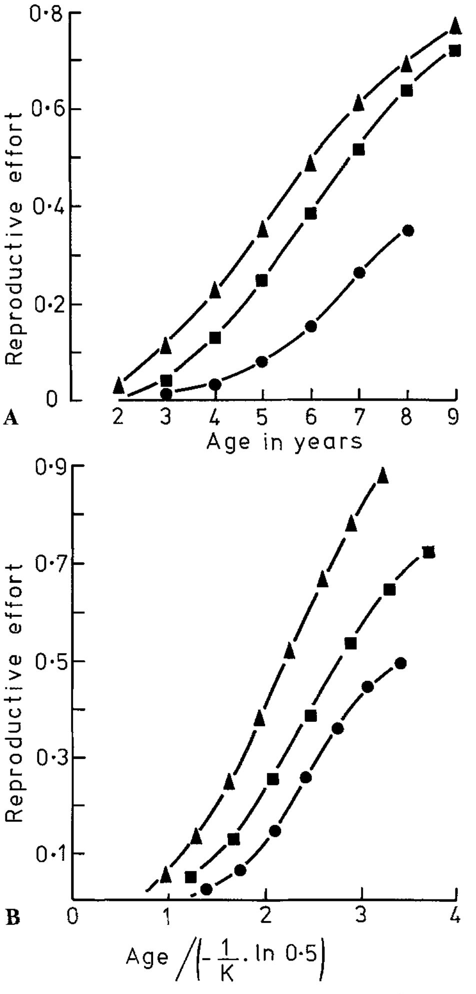

Fig. 1. **A** Reproductive effort, measured as $P_r/(P_r+P_g)$, in *Mytilus edulis* at three sites, related to age; ▲, Lynher (1973/'75); ■, Mothecombe; ●, Cattewater. **B** As in A, but with the age axis corrected (see text) to exclude differences due to different rates of growth

that spawning weight loss is isometric to total body weight; estimates in Table 2 and 3 were adjusted accordingly.

2. Reproductive effort (R.e.)

R.e. based on age-related weight changes and on estimates of weight loss on spawning. Calculations have been made for mussels from three sites, Lynher and Cattewater (from Bayne and Worrall 1980) and Mothecombe. Reproductive effort $[P_r/(P_r+P_g)]$ increased with age (Fig. 1 A) but whereas mussels from Mothecombe and Lynher yielded similar values, those from the Cattewater had a much reduced effort. Hughes and Roberts (1980) suggested a transformation of the independent variable (age) to exclude, from comparisons such as this, differences due simply to different rates of growth. Values for P_r/P are re-plotted in Fig. 1 B against age as "years$\left(-\frac{1}{K}\cdot\ln 0.5\right)$" where K is the rate constant in the von Bertalanffy growth equation for each site. The result is to rank mussels from the three sites in order of increasing reproductive effort: Cattewater < Mothecombe < Lynher.

R.e. based on physiological estimation of P. Physiological measurements and estimates of food availability were made on five occasions at four sites (Lynher, Kings Dock, Swale and Mumbles). As expected (Bayne and Widdows 1978) there were seasonal changes at all sites. For present purposes, however, mean values were determined for available ration (Table 4) and for absorption efficiency (Table 5). Regression analysis, involving all available data, was used to derive allometric equations to relate clearance rate (as $\mathrm{l\cdot h^{-1}}$) and oxygen consumption (as $\mathrm{cm^3\cdot h^{-1}}$) to dry flesh weight (in grams) for mussels from each site (Table 5). The absorbed ration, $A(=C\cdot e)$, was calculated as clearance rate × ration × absorption efficiency. The metabolic loss term, R, was calculated as oxygen consumption × the oxycaloric coefficient (20.08 $\mathrm{J\cdot cm^{-3}\ O_2}$). Gamete production was derived from relationships stated earlier (Tables 2 and 3) and reproductive effort evaluated as $P/(A-R)$. The results (Fig. 2) illustrate a steep rise in reproductive effort with increase in body weight. Large differences between sites are also evident; a mussel of dry flesh weight 0.7 gram may vary by × 10 in its reproductive effort (2–20%) depending on its site of origin.

A comparison of reproductive effort values calculated from estimates of growth and from physiological determinations. This comparison is possible for mussels from the Lynher and Cattewater sites. The result (Fig. 3) suggests that physiological determinations may underestimate reproductive effort; however, the agreement between the two methods of calculation is reasonable considering the different assumptions and errors involved.

Table 4. The composition of suspended particulate organic matter (POM) at four sites, averaged over five sampling periods during 1976/'77. The ration available to mussels is estimated using the energy equivalents 23.6 J mg^{-1} (protein), 17.2 J mg^{-1} (carbohydrate) and 39.5 J mg^{-1} (lipid). Values are means ± S.D.

Site	POM ($mg \cdot l^{-1}$)	Proportional composition of POM			Available ration (Joules l^{-1})
		Protein	Carbohydrate	Lipid	
Lynher	1.24 ± 0.63	0.62 ± 0.17	0.27 ± 0.13	0.11 ± 0.07	29.2
Kings Dock	1.09 ± 0.48	0.53 ± 0.13	0.31 ± 0.17	0.12 ± 0.10	24.6
Swale	2.01 ± 0.73	0.56 ± 0.12	0.34 ± 0.08	0.10 ± 0.04	46.2
Mumbles	1.45 ± 0.44	0.49 ± 0.09	0.42 ± 0.15	0.09 ± 0.02	32.5

Table 5. The results of physiological measurements made on *M. edulis* from four sites between May 1976 and May 1977. Clearance rates and oxygen consumption rates are quoted as regression equations relating the measurements to dry flesh weight (W; grams). Values are quoted ± S.D.

Site	Clearance rate ($l \cdot h^{-1}$)	Absorption efficiency	Oxygen consumption ($cm^3 \cdot h^{-1}$)
Lynher	$1.27\ (\pm 0.31) \cdot W^{0.372\ (\pm 0.081)}$	$0.30\ (\pm 0.02)$	$0.457\ (\pm 0.178) \cdot W^{0.667\ (\pm 0.060)}$
Kings Dock	$1.15\ (\pm 0.12) \cdot W^{0.443\ (\pm 0.103)}$	$0.44\ (\pm 0.12)$	$0.591\ (\pm 0.221) \cdot W^{0.550\ (\pm 0.104)}$
Swale	$1.49\ (\pm 0.37) \cdot W^{0.488\ (\pm 0.102)}$	$0.23\ (\pm 0.13)$	$0.748\ (\pm 0.257) \cdot W^{0.695\ (\pm 0.071)}$
Mumbles	$1.69\ (\pm 0.82) \cdot W^{0.316\ (\pm 0.142)}$	$0.27\ (\pm 0.06)$	$0.687\ (\pm 0.097) \cdot W^{0.482\ (\pm 0.114)}$

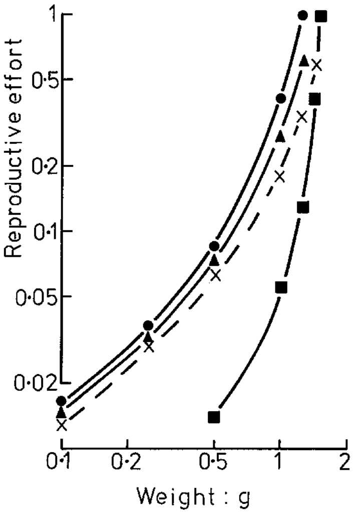

Fig. 2. Reproductive effort, measured as $P_r/(A-R)$, in *Mytilus edulis* from four sites, related to dry flesh weight. ●, Swale; ▲, Kings Dock; ×, Lynher (1976/'77); ■, Mumbles

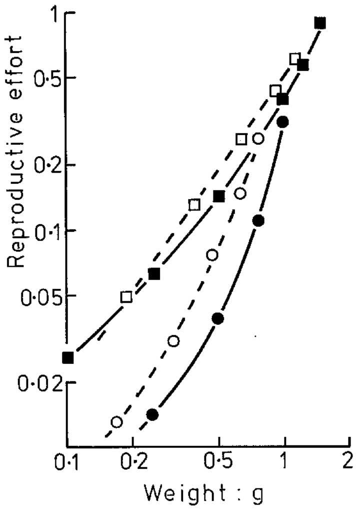

Fig. 3. Reproductive effort in *Mytilus edulis* from two sites, related to dry flesh weight. □, Lynher; ○, Cattewater, both measured as $P_r/(P_r+P_g)$. ■, Lynher; ●, Cattewater, both measured as $P_r/(A-R)$

3. The energetic costs of reproduction

In Fig. 4 estimates of respiratory energy loss by mussels at two sites, derived from measurements of oxygen consumption, are related to an index of gametogenesis (the "gamete volume fraction" or GVF), which is based on the stereological analysis of germinal tissue in the mantle (Bayne and Widdows 1978; Lowe et al. 1982). Values for R at low levels of GVF are taken to represent the energy demands of somatic maintenance i.e. R^* in Eqs. (4) and (5). A similar, but less detailed analysis was possible for two other sites, Swale and Mumbles, where oxygen consumption determinations were made at both a high and a low level of GVF (before and after spawning, respectively) at times when temperature and ration conditions were similar (Table 6). Taking these four sites, the following relationships emerge between R^* and total respiratory heat loss, R:

Lynher: $R^* = 0.57 \cdot R$
Cattewater: $R^* = 0.78 \cdot R$
Swale: $R^* = 0.60 \cdot R$
Mumbles: $R^* = 0.72 \cdot R$

These values for R^* (and for $R - R^*$) were used to calculate a cost index, C (Eq. (5)), which is plotted against body weight in Fig. 5. At all sites C increased with increase in size; for most of the size range C took negative values,

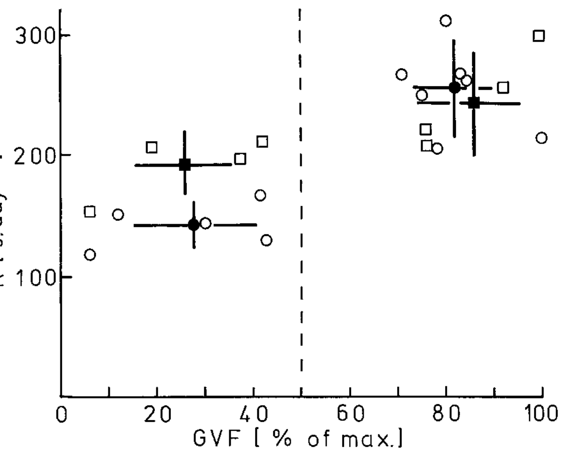

Fig. 4. Respiratory energy loss by *Mytilus edulis* from two sites, related to an index of gametogenesis, *GVF* (see text). The open symbols are measurements made in the Lynher (o) and Cattewater (□). The closed symbols are means (±S.D.) for values less than and greater than 50% of maximum GVF

Table 6. Rates of oxygen consumption associated with high and low gamete volumes in *Mytilus* at two sites. Gamete volumes were calculated from the gamete volume fraction (GVF) and the volume of the mantle tissue, measured by displacement. Rates of oxygen consumption are quoted as regression equations relating consumption to dry flesh weight (*W*; grams). Means flesh weights at the two sites were 0.520 g (Swale) and 0.795 g (Mumbles)

Site	Month	Gamete volume (mm^3)	Rate of oxygen consumption: $cm^3 \cdot h^{-1}$
Swale	May	64 ± 7	$0.984\ (\pm 0.049) \cdot W^{0.695}$
	November	4 ± 1	$0.600\ (\pm 0.075) \cdot W^{0.695}$
Mumbles	July	135 ± 26	$0.652\ (\pm 0.042) \cdot W^{0.482}$
	October	3 ± 1	$0.469\ (\pm 0.103) \cdot W^{0.482}$

consistent with the prediction (Calow 1979) that the production of gametes in an iteroparous, planktotrophic bivalve would be "restrained" i.e. that gametogenesis would not occur at the expense of somatic maintenance. However, the largest mussels showed more "reckless" gamete production, with the full energetic costs equalling ($C = 0$) or exceeding ($C > 0$) the demands of maintenance. It appears also that in comparing the Cattewater with the Lynher, mussels from the former site show reduced reproductive effort (Fig. 1A) but at greater cost than those from the latter site. Equally, mussels from Mumbles show reduced effort (Fig. 2) compared with those from the Swale, but at greater cost, at least in the smaller individuals.

However, these high costs seem largely to be due to high respiratory demands for maintenance i.e. R^* values are a greater proportion of total respiratory loss at Cattewater and Mumbles than at the other two sites. In Fig. 6 calculated energy demands for reproduction ($R - R^*$) are plotted against P_r, which was derived from determinations of weight loss on spawning. The data are consistent with a single relationship, suggesting that the energy demands associated with different levels of reproduction may be similar at different sites.

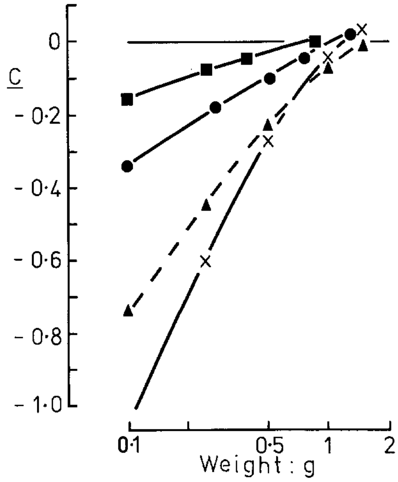

Fig. 5. An index of reproductive cost, *C* (see text) for *Mytilus edulis* from four sites, related to dry flesh weight. ■, Cattewater; ●, Lynher; ▲, Mumbles; ×, Swale

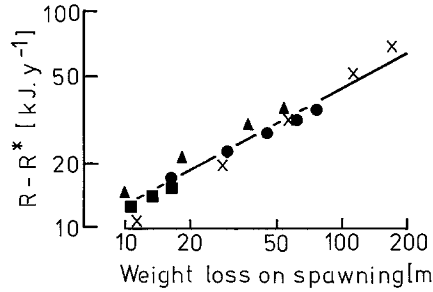

Fig. 6. The calculated energy demands of gametogenesis in *Mytilus edulis* from four sites, related to mean weight loss on spawning. Symbols as for Fig. 5. Values for weight losses at Mumbles are derived from direct estimates of fecundity (Table 2) assuming a weight exponent of 1.0. Weight losses at the other sites are from indirect estimates (Table 3)

Table 7. Annual mortality of mussels at three sites. The regression equations relate the logarithm of numbers per square meter (*N*) to mean shell length (*L*). The mortality is estimated from the slopes of these regressions and parameters of growth, according to Van Sickle (1977). In all three cases data from five year classes were used in calculating the regression equations, and correlation coefficients (r^2) for the regressions were all > 0.95

Site	Equation relating nos·m^{-2} to mean shell length for different age classes	Calculated annual % mortality
Lynher	$\ln N = 6.84 - 0.051 \cdot L$	54
Mothecombe	$\ln N = 7.64 - 0.056 \cdot L$	60
Cattewater	$\ln N = 10.93 - 0.106 \cdot L$	72

4. Reproductive value

The regression equations used in calculating mortality ($\ln N = a - nL$; where N is number of individuals m^{-2} and L is shell length in mm) and the values for annual mortality (as percent) are listed in Table 7 for three sites. Mortality was greatest at the Cattewater, a finding consistent with

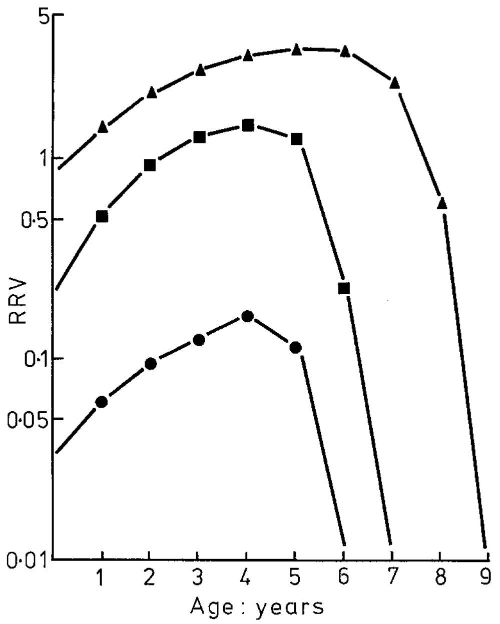

Fig. 7. The residual reproductive value (*RRV*) of *Mytilus edulis* from three sites, related to age. ▲, Lynher; ■, Mothecombe; ●, Cattewater

the high levels of environmental stress at this site (Bayne and Widdows 1978). In using these estimates to calculate residual reproductive value, the assumption is made that mortality is constant over all ages greater than one year post-settlement.

At all three of these sites residual reproductive value (RRV) increased with age to maximum values between four and six years (Fig. 7). There were marked differences between sites, however, in the level of RRV attained. Relationships of this shape (see also Vahl 1982) between RRV and age represent an inevitable consequence of increasing reproductive effort with age, together with an (assumed) constant and age-independent mortality. The population differences evident in Fig. 8 represent increased mortality at Mothecombe (marginally) and Cattewater, relative to Lynher, and a marked depression of reproductive effort at the Cattewater site.

Discussion

It is not surprising that individuals of the same species (*M. edulis*) from different habitats (or from the same habitat but in different years cp. Lynher 1973/75 and 1976/77) should differ in various aspects of reproductive effort and behaviour, given the wide range of environmental conditions normally encountered and tolerated. For the individuals and habitats considered in this study, for example, annual fecundity, reproductive effort (measured as the proportion of total production allocated to the production of gametes) and maximum reproductive value all varied by up to an order of magnitude between individuals at different sites. On the other hand, other aspects of the reproductive strategy of the species were less variable between sites. For example, egg sizes did not differ significantly; the metabolic costs for a similar magnitude of gamete production were similar; there was a basic isometry between gamete production and body weight; reproductive effort increased in all cases with an increase in age; and residual reproductive value increased to a broad "plateau" of maximum values, encompassing similar year classes at different sites, before declining sharply to zero. Earlier experimental results (see Bayne et al. 1982a) had also indicated that high temperature and reduced ration in the laboratory caused a reduction in fecundity but only resulted in reduced egg weights when the stress took extreme values. In these experiments also, reproductive effort was reduced in response to increased stress.

Theoretical considerations, based on optimality principles (Sebens 1982) suggest that an animal should divert energy from somatic growth to the production of offspring when the difference between energy absorbed and metabolic loss is greatest. The generality of this statement is expected to be modified under at least two conditions; firstly, in animals of indeterminate growth, the switch from growth to reproduction may occur gradually (Calow 1981), and secondly, particular morphological constraints may limit the space available for development of the gonad and so shift the switch from the theoretical optimum to a greater body size (Sebens 1982). *Mytilus edulis* illustrates the first of these conditions (Theisen 1968, 1973; Seed 1976) and probably the second also, since the volume available for gonad development in the mantle tissue will be limited by the rate of increase in the volume of the mantle cavity. Brown et al. (1976) recorded a positive allometry between shell length, shell width and shell weight in inter-tidal *Mytilus edulis*.

The data in Fig. 8A illustrate agreement with theoretical predictions in that the mean body weight of individuals at the time of the maximum rate of increase in reproductive effort (see Fig. 1A) occurs slightly to the right of the size at which there is maximum scope for growth and gamete production. Also, individuals from a site experiencing high water temperatures in the winter, with consequent physiological stress (Cattewater) express this maximum rate of increase in reproductive effort at a smaller body size than individuals from a less stressed site (Lynher). Furthermore, the maximum residual reproductive value occurs at the age of maximum rate of growth (Fig. 8B) except possibly in the Cattewater, where maximum RRV appears shifted slightly towards younger individuals. In terms of these more fundamental aspects of reproductive strategy, therefore, mussels from very different habitats show a unity of response that presumably reflects ultimate evolutionary considerations for the species.

Theoretical predictions for relationships between reproductive behaviour and degrees of environmental stress are less clear and particularly difficult to evaluate in a species with a widely dispersive larval stage. Nevertheless, the results of this study suggest that in response to environmental deterioration *Mytilus* reduces its age-specific reproductive effort. Indeed, a comparison of mussels from the three sites Lynher, Mothecombe and Cattewater illustrates a graded series of increasing mortality, decreasing rates of growth and declining reproductive effort. Theoretical considerations by Goodman (1979) anticipate a decline in reproductive effort (measured as a ratio between natality and survivorship) with environmental deterioration for species in which the young are more sensitive to environmental influences than older year classes and in which "adult survival rates are buffered against the effects of environmental change relative to the capacity for reproduction" (p. 746).

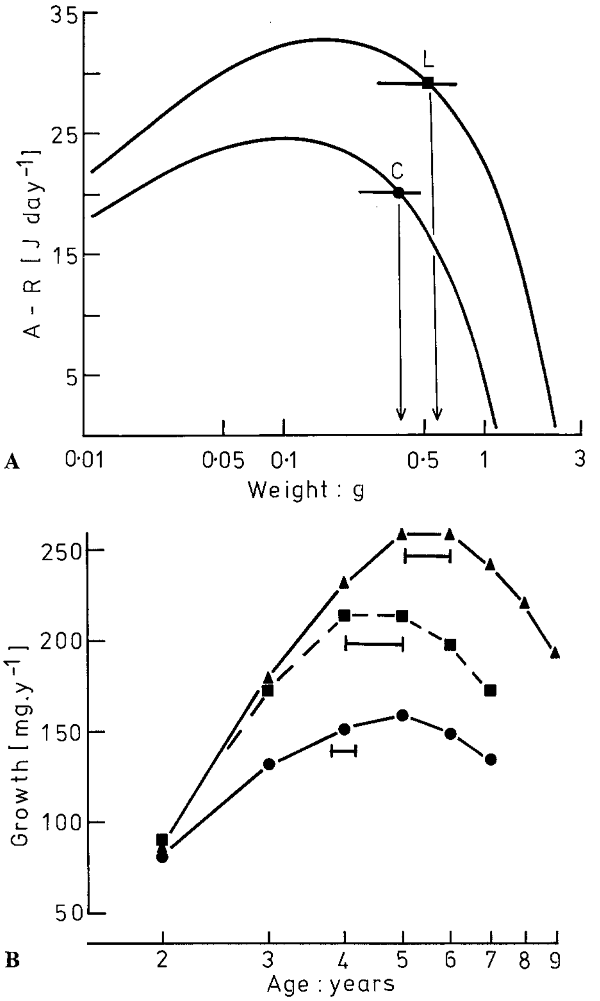

Fig. 8. A The scope for growth (absorbed energy, *A*, minus respiratory energy loss, *R*) in *Mytilus edulis* from two sites, Lynher (*L*) and Cattewater (*C*), related to dry flesh weight. The mean weights at which annual, age-related, increase in reproductive effort is most rapid (see Fig. 1A) are indicated (mean ± range) for individuals from each site. **B** The rates of growth (mg dry flesh per annum) of *Mytilus edulis* from three sites, related to age in years. ▲, Lynher; ■, Mothecombe; ●,Cattewater. The ages of maximum residual reproductive value (see Fig. 7) for mussels at each site are indicated as bars

Small (putatively young) mussels have a higher metabolic rate and a higher maintenance energy requirement (measured as % body weight day^{-1}) than larger (older) mussels. Although smaller mussels have a higher maintenance efficiency than larger individuals, this does not compensate fully for differences in the maintenance requirement and smaller mussels consequently lose weight (as % body weight day^{-1}) more rapidly during starvation than larger mussels (Bayne and Newell 1983). Newell and Bayne (1980) recorded an allometric relationship between total carbohydrate content and dry-tissue weight in *Cardium (Cerastoderma) edule;* the exponents for this relationship varied seasonally but were, for the most part, > 1.0, suggesting positive allometry (see also Holland and Hannant 1976, for *Ostrea edulis*, and Sundet and Vahl, 1981, for the Iceland scallop, *Chlamys islandica*). If the same is true for *Mytilus*, and given an exponent value of < 1.0 relating metabolic rate to body size (Table 5), then the glycogen store represents a greater buffer against periods of reduced ration in larger than in smaller individuals. Studies have indeed documented that small bivalves catabolise more protein during periods of food shortage, relative to losses of carbohydrate, than larger individuals (Bayne and Scullard 1977; Newell and Bayne 1980; Vahl 1982). These findings all point to smaller individuals being more vulnerable, in energetic terms, to periods of reduced ration than larger individuals. Small mussels are also more vulnerable to predation (Paine 1976).

Finally, studies of gamete production by individuals under stress from environmental factors demonstrate that gametogenesis occurs only when sufficient resources are available above the requirements of somatic maintenance, to ensure the survival of the adult (Bayne et al. 1982b; Newell et al. 1982). Reproduction in *Mytilus edulis* is increasingly "reckless" (Calow 1979) with age, but the overall strategy is one of "restraint" (Fig. 6). These are properties consistent with Goodman's (1979) predictions. The extent to which variability in the different aspects of reproductive behaviour considered here may represent different "tactics" in the sense of Stearns (1976, 1980), requires better life table data for the species in a variety of well defined environmental situations.

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