Production, reproductive effort, reproductive value and reproductive cost in a population of the blue mussel *Mytilus edulis* from a subarctic environment

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ABSTRACT: The standing crop of mussels *Mytilus edulis* from Bellevue, Newfoundland, is similar to that of the densest beds in warmer waters, but population production is not as great. Production by individual mussels at Bellevue exceeds that in most populations for which appropriate data are available. Detailed comparison with a population in the Lynher estuary, southwest England, confirms previous conclusions, based on physiological measurements, that Lynher mussels experience greater stress than Bellevue mussels, despite the considerable temperature advantage enjoyed by the former. Expression of growth in terms of day-degrees suggests that there is no meaningful analysis based on temperature alone. Reproductive effort is high in *M. edulis* at Bellevue, reaching 0.94 in the oldest individuals. Residual reproductive value attains a maximum at 3 to 4 yr, after which it decreases rapidly.

INTRODUCTION

During the last decade, several studies have considered not only the individual physiological rate functions of mytilid bivalves but also the integrated response. Much of this literature, reviewed by Bayne et al. (1976), is concerned with experiments in which controlled algal diets were used. More recently the emphasis has shifted towards studies under more natural conditions, especially with the growing recognition that the nature and concentration of particles in suspension are major determinants of the observed response (Bayne and Widdows, 1978; Thompson, 1984). Studies of growth and production have followed, in order to complement physiological work and to provide a broader base for understanding the performance of the animal in the environment.

In a companion paper (Thompson, 1984) I describe the physiological ecology of the blue mussel *Mytilus edulis* from Bellevue, Newfoundland. A detailed comparison is made with homologous data from southwest England (Bayne and Widdows, 1978). Despite the much lower temperature regime in the subarctic Labrador current, Bellevue mussels have a higher growth efficiency than those from the Lynher estuary in Corn-

wall, and it appears that the latter are under greater stress than the former. In the present paper I demonstrate that these physiological differences are reflected in enhanced growth and gamete production by the Bellevue population, and that population biomass and production are high at the Newfoundland site.

This study also deals with reproductive effort (that proportion of the net energy available which is used for reproduction) and reproductive value (the average expected lifetime fecundity). Recently, however, there has been a tendency to dismiss reproductive effort as being of little importance in life history theory (Bell, 1980), the emphasis moving to reproductive value, which is regarded as a better fitness correlate (Goodman, 1982). Nevertheless, whether or not reproductive effort plays a significant role in the analysis of life history strategies, it remains a useful index to describe the partitioning of energy into growth and reproduction, and it also provides a good basis for comparisons between populations in terms of responses to stress (Bayne et al., 1983). These authors have also drawn attention to the paucity of data on intraspecific variation in quantities such as reproductive effort, reproductive value and reproductive cost. The gradual accumulation of an appropriate body of data for mytilids in

various parts of the world affords us the opportunity to seek diversity or uniformity of response in different habitats.

MATERIALS AND METHODS

The data presented here were obtained from a sublittoral population of mussels at Bellevue, Newfoundland. A description of the habitat has been provided elsewhere (Thompson, 1984).

Growth in both shell length and dry flesh weight was expressed as a function of age, determined as follows. Qne valve from each specimen was sectioned along the antero-posterior axis with a diamond-tipped circular saw blade. It was not found necessary to embed the valve in epoxy resin. The thick section was polished with no. 320 and no. 600 silicon carbide grit, followed by no. 175 optical finishing powder, then examined in a dissecting microscope under reflected light. Shell growth lines were interpreted as described by Lutz (1976). In older shells resolution of the most recent growth lines was sometimes improved by inspection of acetate peels prepared according to Rhoads and Pannella (1970).

A growth curve was fitted according to the von Bertalanffy function:

$$l_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \qquad (1)$$

where l_t = length at time t; L_∞ = mean asymptotic length; K = Body growth coefficient; t_0 = a parameter representing time when l_t = 0. The parameters K and L_∞ were derived from a Ford-Walford plot of l_{t+1} against l_t (Ricker, 1975).

Growth was also considered in terms of day-degrees, an integration of temperature over time, by means of a modification of the von Bertalanffy model (Ursin, 1963):

$$l_D = L_\infty \left(1 - e^{-K_D(D-D_0)}\right) \qquad (2)$$

where l_D = length at D day-degrees; $K_D = K/D_y$ (D_y = annual sum of day-degrees); $D_0 = t_0 \cdot D_y$.

Somatic growth (P_g) was obtained for each age class from annual increments in dry flesh weight $W_{(x+1)} - W_x$ (1 g dry weight = 21.8 kJ; Bayne and Worrall, 1980). The organic component of the shell was disregarded, since it forms only 3 % of the shell weight (own unpubl. obs.), and represents less than 2 % of the production by the mussel. The weight lost on spawning, calculated from equations given by Thompson (1984), was used as an estimate of gamete production (P_r) (1 g dry eggs = 23.0 kJ; Bayne et al., 1975). Reproductive effort was then given by the expression $P_r/(P_g + P_r)$.

Calow (1979) has proposed the following index of reproductive cost:

$$\text{Cost} = 1 - \left[\frac{(C.\ e) - P_r}{R^\bullet}\right] \qquad (3)$$

where C = ingested ration; e = absorption efficiency; $R^\bullet$ = metabolic demand of the somatic tissue (n. b. Calow's original notation is different). This index has been modified by Bayne et al. (1983) to incorporate a term ($R-R^\bullet$, where R = total metabolism) which defines the energy demands of gametogenesis:

$$\text{Cost} = 1 - \left[\frac{(C.\ e) - (P_r + R - R^\bullet)}{R^\bullet}\right] \qquad (4)$$

Data from another study (Thompson, 1984) were used to calculate ingested ration, mean absorption efficiency and total metabolism for 1 yr. The energy content of the total particulate matter was taken as 3.31 J mg^{-1} (MacDonald and Thompson, unpubl., from which a mean value of 14.1 J l^{-1} was obtained for food availability. In order to estimate $R^\bullet$, the reproductive cycle was considered as comprising 2 phases, a gametogenic and spawning phase, and a non-gametogenic ('resting') phase (Thompson, 1984). Integration of oxygen uptake over time during the 'resting' period provided a mean metabolic rate for somatic maintenance which was then applied to the whole year, giving $R^\bullet$ (1 ml O$_2$ ≡ 19.9 J). Reproductive cost was calculated by substitution in Equation (4).

Williams (1966) partitioned reproductive value into 2 terms, the first representing current fecundity (m_x), the second the residual reproductive value (RRV), i.e. the future reproductive potential of an organism at age x:

$$\text{RRV} = \sum_{t=x+1}^{\omega} \frac{l_t}{l_x} m_t \qquad (5)$$

where l_t/l_x = probability of survival from age x to age t; ω = age of last reproduction; m_t = fecundity at age t. In this study, I have expressed RRV in terms of gamete production, i.e. energy units, rather than fecundity *per se*. The life table parameter l_t/l_x was determined directly as follows. Twenty quadrats (0.1 m^2) were thrown at random and the mussels in each counted. The length of each mussel was measured and its age estimated from the growth curve described previously. An age-frequency distribution was thereby obtained. This procedure was repeated exactly 1 yr later, and a survivorship curve constructed.

RESULTS

Growth

The validity of the technique for age determination was demonstrated in sections from the shells of cul-

tured *Mytilus edulis* of known age which confirmed that the growth lines are laid down annually (Lutz, 1976).

Growth in shell length (cm) was expressed by the von Bertalanffy function:

$$l_t = 10.86 \, [1-e^{-0.192(t-0.347)}] \qquad (6)$$

The von Bertalanffy curve described growth well in older mussels, but there appeared to be a sigmoidal phase in the growth of younger ones (Fig. 1). Of the 3-parameter models available, however, the von Bertalanffy provided the best fit and proved adequate for present purposes, although in future work, where direct comparisons are being made between growth rates in different populations, it may become desirable to explore 4-parameter treatments.
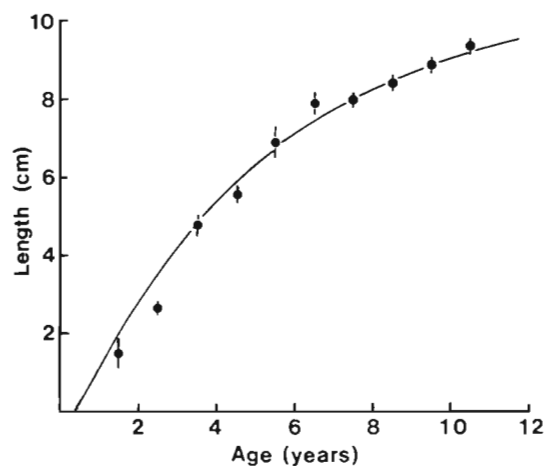
Fig. 1. *Mytilus edulis.* Growth curve for individuals from Bellevue, Newfoundland. Mean ± 95 % C. L.

At Bellevue the annual sum of day-degrees (D°) was 2241 (calculated from a baseline at 0 °C). Modification of the von Bertalanffy equation to incorporate the temperature factor resulted in

$$l_D = 10.86 \, [1-e^{(-0.86 \times 10^{-4}) \, (D-778)}] \qquad (7)$$

Growth in maximum dry flesh weight (somatic plus reproductive tissue) was more rapid than growth in somatic tissue alone (Fig. 2). Mussels from Bellevue may become very large; immediately before spawning, a 10 yr old individual is 9 cm long and weighs 5.5 g. Comparable data for *Mytilus edulis* from the Lynher estuary, southwest England, are also presented (Bayne and Worrall, 1980).

Production by individual mussels

Somatic production (Pg) increased yearly in mussels younger than 6 yr, but gradually decreased in older

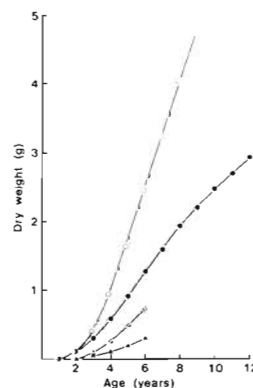individuals (Fig. 3). Gamete production (Pr), however, continued to increase throughout the life of the mussel.

Fig. 2. *Mytilus edulis.* Growth in dry flesh weight of individuals from Bellevue (circles) and the Lynher estuary (triangles). Closed symbols: January; open symbols: June. Lynher data from Bayne and Worrall (1980)
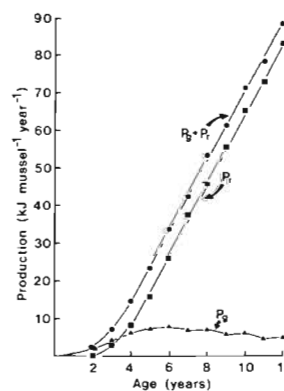
Fig. 3. *Mytilus edulis.* Somatic production (P_g; ▲), gamete production (P_r; ■) and total production (P_g + P_r; ●) in individuals from Bellevue

Reproductive effort

The reproductive effort of Bellevue mussels was an increasing function of age, reaching a maximum of 0.94 in animals 12 yr old (Fig. 4). Values for Lynher mussels (Bayne and Worrall, 1980) are included for comparison.

Population density, biomass and production

The age-frequency distribution was bimodal (Fig. 5). Quantitative sampling of spat was not possible, so the first of the 2 peaks could not be resolved, but the second mode at 5 yr was clear. The mean number of mussels (> 3 mm) per 0.1 m^2 quadrat was 78 (95 % CL = 13.1, n = 20) i.e. the population density was 780 mussels m^{-2}.
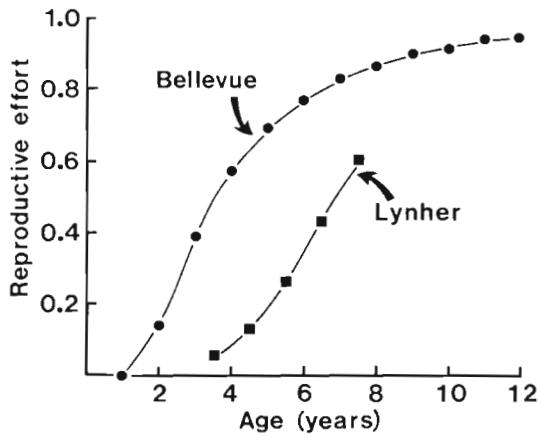
Fig. 4. *Mytilus edulis.* Reproductive effort ($P_r/(P_g + P_r)$) in individuals from Bellevue (●) and the Lynher (■). Lynher data from Bayne and Worrall (1980)
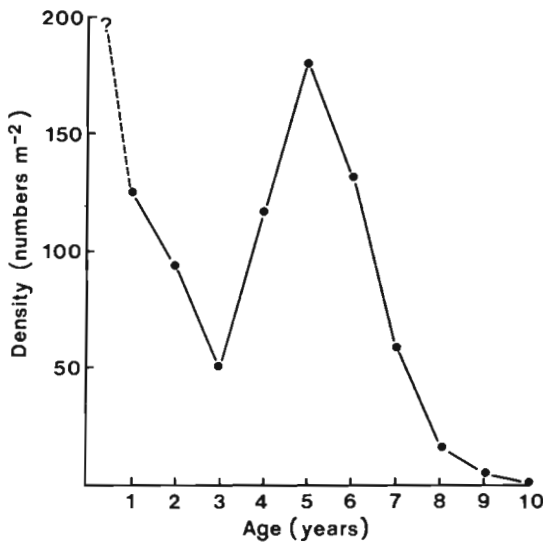

Fig. 5. *Mytilus edulis.* Population density of Bellevue mussels
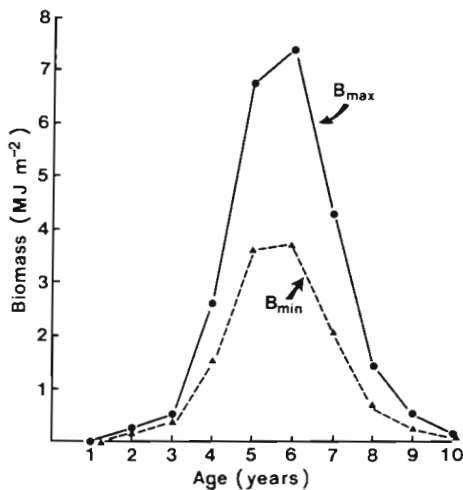

Fig. 6. *Mytilus edulis.* Biomass of mussels at Bellevue. ● maximum biomass (June); ▲ minimum biomass (January)

Three quarters of the population biomass (B) was accounted for by mussels 4 to 7 yr old (Fig. 6). The maximum standing crop (June) was 23.9 MJ m^{-2} (equivalent to 1.07 kg dry flesh weight m^{-2}), approximately twice the minimum value (January).

Individuals aged from 4 to 7 yr also contributed three-quarters of both somatic and gamete production by the population (Fig. 7).
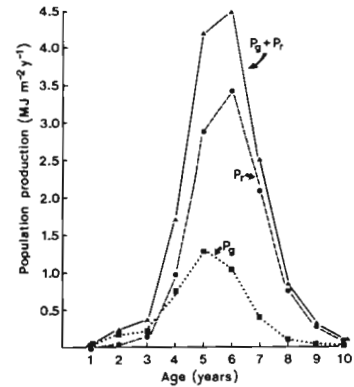

Fig. 7. *Mytilus edulis.* Production by the population at Bellevue. ■ somatic production (P_g); ● gamete production (P_r); ▲ total production ($P_g + P_r$)

The turnover ratio, or production: biomass ratio, may be calculated for somatic production only (P_g/B) or for total production ($(P_g + P_r)/B$). The former is more commonly used in studies of population dynamics, but both are of interest here. As a consequence of decreased somatic production in older individuals, $P_g/\overline{B}$ in Bellevue mussels fell from a maximum (0.82) at 2 yr to 0.07 at 10 yr (Fig. 8). When gamete production was taken into account, however, turnover ratio was independent of age for animals greater than 4 yr old.
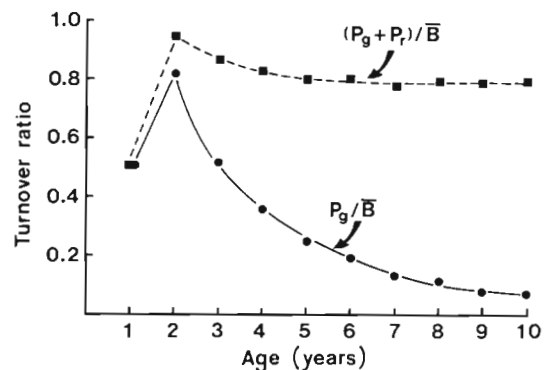

Fig. 8. *Mytilus edulis.* Turnover ratios in Bellevue mussels ■ total production/mean biomass; ● somatic production/mean biomass

Mortality and residual reproductive value

Mortality was high in the first 2 yr of life, and in the last 4 yr (Fig. 9). At intermediate ages, however, there was little mortality (fourth to fifth year, $M = 0.16$; fifth to sixth year, $M = 0.05$). The highest mortality rates (0.91) were found in mussels 9 and 10 yr old. The relation between residual reproductive value and age (Fig. 10) strongly reflected the underlying survivorship curve, and mussels of intermediate age possessed the greatest RRV.
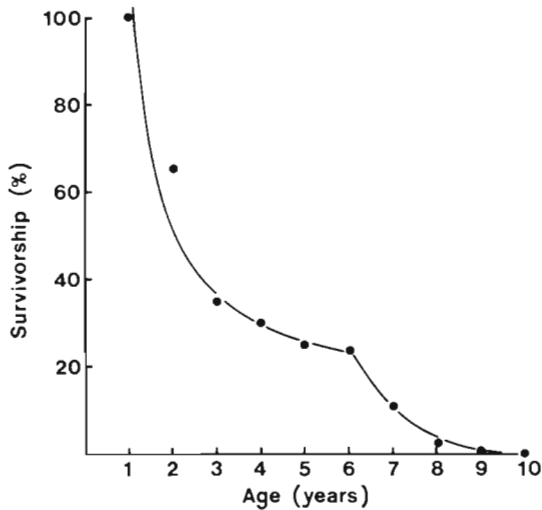

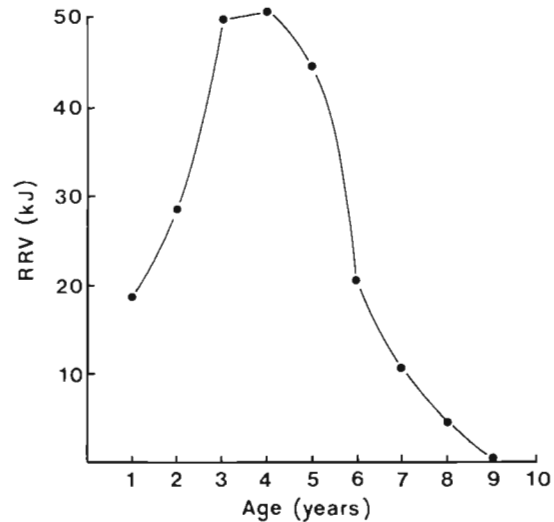Fig. 9. *Mytilus edulis.* Survivorship curve at Bellevue

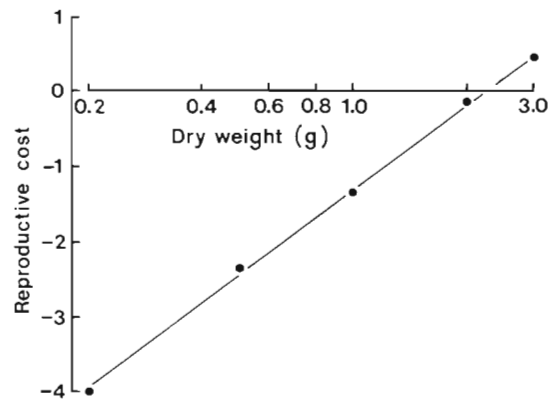Fig. 10. *Mytilus edulis.* Residual reproductive value as a function of age at Bellevue

Fig. 11. *Mytilus edulis.* Relations between an index of reproductive cost and dry flesh weight in mussels from Bellevue

Reproductive cost

The metabolic demands of somatic tissue (R^*) accounted for 81 to 84 % of total metabolism (R) in mussels from 0.2 to 1.0 g dry weight, but somewhat less in larger individuals (Table 1). Reproductive cost increased linearly with the logarithm of dry weight (Table 1; Fig. 11). Only in very large $(> 2.3$ g), senescent mussels did the cost of reproduction exceed maintenance demands.

DISCUSSION

The standing crop of mussels *Mytilus edulis* at Bellevue is very high, and compares favourably with that of *M. edulis* and other mytilids from warmer locations such as the Irish Sea, Rhode Island and the coast of

Table 1. *Mytilus edulis.* Estimation of reproductive cost

Dry wt. (g)	C. e (kJ yr⁻¹)	P_r (kJ yr⁻¹)	R (kJ yr⁻¹)	R* (kJ yr⁻¹)	R-R* (kJ yr⁻¹)	R*/R	Reproductive cost
0.2	50.0	4.0	10.8	8.77	2.06	0.81	−4.0
0.5	73.9	6.5	22.4	19.1	3.30	0.85	−2.4
1.0	99.2	18	38.0	31.9	6.10	0.84	−1.3
2.0	133	48	76.3	57.7	18.6	0.75	−0.15
3.0	158	83	111	80.3	30.7	0.72	0.45

South Africa (Table 2). The similarity between biomass values for mytilids from such a variety of favourable habitats supports a contention expressed by Dare (1976) that there is a 'carrying capacity' for an environment suited to mussels, although in marginal environments, such as the Baltic, biomass and production are greatly reduced (Kautsky, 1982). Production by the mussel bed at Bellevue, however, is considerably

but are confounded by the fact that this quantity is a decreasing, non-linear function of age (7.6 mm/1000 D° at 2 yr, 3.6 at 6 yr, 1.8 at 9 yr in the Bellevue population). Interpretation of such data as a basis for meaningful comparisons between populations presents an intractable problem, owing to our inadequate knowledge of the factors which influence shell growth. There is a need to place less emphasis on the analysis

Table 2. Production and biomass in mytilids from several locations

Species	Locality	Biomass (MJ m^{-2})	Total production (MJ m^{-2} yr^{-1})	Longevity (yr)	Maximum length (cm)	Source
Mytilus edulis	Bellevue, Newfoundland	13–24	11	12	11	Thompson (this study)
Mytilus edulis	Morecambe Bay, U. K.	28	~ 80	3	–	Dare (1976)
Mytilus edulis	Baltic Sea	~ 2.2	–	(14)	7	Kautsky (1982)
Mytilus edulis	Rhode Island	34	–	–	–	Nixon et al. (1971)
Choromytilus meridionalis	South Africa	15–22	100	(15)	10	Griffiths (1977, 1981)
Perna perna	South Africa	18–28	157	3	12	Berry (1978)
[Macrobenthos	North Sea	0.025–0.067	0.08–0.21	–	–	Steele (1974)]

lower than that observed in populations in Morecambe Bay and in South Africa (Table 2). As Dare (1976) points out, mussel beds may be extremely productive-both biomass and production greatly exceed typical values for the benthos in the North Sea, for example (Steele, 1974). There is a remarkable similarity between the standing crop of *M. edulis* from Newfoundland and that of *Choromytilus meridionalis* from a population in Cape Province, South Africa (Griffiths, 1981).

Seed (1976) remarks on the general absence of polymodal size-frequency distributions in *Mytilus*, but examinations of several populations of *M. edulis* from Newfoundland have confirmed that the bimodal distribution observed at Bellevue appears to be general (Sutterlin et al., 1981). The Bellevue population is dominated by mussels 5 to 6 yr old. In Natal, South Africa, populations of the short-lived, fast-growing mytilid *Perna perna* exhibit bimodal or trimodal size-frequency distributions (Berry, 1978).

The literature on shell growth in mytilids is extensive and has been reviewed by Seed (1976), Bayne and Worrall (1980) and Lutz (1980). There is considerable variation in growth rates, and attempts have been made to interpret growth data in terms of day-degrees (D°). Thus according to studies reviewed by Seed (1976), *Mytilus edulis* requires approximately 6000 D° to attain a length of 5 cm in the Danish Waddensea, 5000 D° in the Menai Straits, 15 000 D° at Conwy and 9000 D° at Disko Bay, Greenland. At Bellevue the comparable figure is 6700 D°, whereas in the Lynher estuary it is more than 25 000 (Bayne and Worrall, 1980). Comparisons of $\triangle l$/1000 D° are sometimes made

of growth in shell length, despite its convenience (Seed, 1976), and more on tissue weight, which is more relevant to a consideration of production.

Individual *Mytilus edulis* at Bellevue, Newfoundland, are 5 to 10 times more productive than those of equivalent age from an intertidal population on a rocky shore in the North Sea (values calculated from tissue weights recorded by Seed, 1973), and are also much more productive than mussels from the littoral zone in the Lynher estuary (Bayne and Worrall, 1980) and from the sublittoral in the Baltic (production estimated using data from Kautsky, 1982). Total production of individuals is also greater in the Bellevue population than in subtidal mussels on the west coast of Ireland (P. Rodhouse, pers. comm.).

There is no simplistic interpretation of mytilid growth in terms of temperature alone. For example, Bayne and Worrall (1980) recorded faster growth in Lynher mussels than in those from the nearby Cattewater, despite higher temperatures at the latter site. This observation is inconsistent with the generalisation that growth rates in marine invertebrates are normally positively correlated with temperature within their distributional range (Newell, 1979). Factors other than temperature must be considered, of which the most important, perhaps, is food supply, but there is very little information available in the literature (Seed, 1976). More recent studies have addressed this problem (Bayne and Widdows, 1978; Bayne and Worrall, 1980; Thompson, 1984), and it has been suggested that absorption efficiency and the ratio of organic to inorganic material in the seston may be important factors in the control of growth (Bayne and Worrall, 1980). A

comparison of data from Bellevue and the Lynher lends some support to this interpretation, because absorption efficiency in Bellevue mussels is greater than in those from the Lynher (Thompson, 1984), and the former do not experience the heavy silt concentrations characteristic of the estuarine Lynher site, with the associated reduction in clearance rate (Widdows et al., 1979). Related information is required from a variety of mytilid habitats, e.g. salt marshes, before the relations between growth, production and the nature of the food supply may be more clearly understood. Detailed investigations of the physiology of mussels from very productive populations (Table 2) are likely to be particularly instructive, since a comparison of data from several locations (Thompson, 1984) suggests that there is too little variation in particulate organic matter to account easily for the large differences in production estimates. Physiological stresses experienced by intertidal mussels must also be considered in any comparison with sublittoral populations, and may be responsible in part for the poorer growth and production by Lynher mussels (Thompson, 1984). Finally, there have been few attempts (e.g. Freeman and Dickie, 1979) to examine the genetic component of production, a hitherto neglected aspect which merits greater attention.

The relations between somatic production and shell length and between gamete production and shell length are very similar in *Mytilus edulis* at Bellevue and *Choromytilus meridionalis* in Cape Province (Griffiths, 1981). In *M. edulis* from Bellevue and from the Lynher (Bayne and Worrall, 1980), somatic production reaches an optimum in mussels of intermediate age before declining in older individuals, whereas gamete production continues to increase. Similar observations have been made on the oyster *Ostrea edulis* (Rodhouse, 1978).

An increase in reproductive effort with advancing age appears to be the norm in bivalve species investigated to date, although there is both interspecific and intraspecific variation in absolute values. In several instances data are directly comparable, since many authors have expressed reproductive effort as gamete production divided by total production. Reproductive effort may be very high in older, larger individuals, e.g. 0.94 in the largest specimens of *Mytilus edulis* from Bellevue, Newfoundland; 0.81 in *Aulacomya ater* 8.5 cm long (Griffiths and King, 1979) and in large mussels *(M. edulis)* from Nova Scotia (Thompson, 1979); 0.97 in *Choromytilus meridionalis* 10 cm long (Griffiths, 1981) and more than 0.9 in a 14 yr old mussel *(M. edulis)* from the Baltic Sea (Kautsky, 1982). High values for reproductive effort have also been recorded in *Ostrea edulis* (Rodhouse, 1978) and in the giant scallop *Placopecten magellanicus* (own unpubl. data).

Reproductive effort in subtidal mussels *(M. edulis)* from the west coast of Ireland reaches a maximum of approximately 0.7 at 8 yr (Rodhouse, pers. comm.). However, in the brown mussel *Perna perna*, a short lived species with an extremely high growth rate, relatively little energy is allocated to reproduction (reproductive effort = 0.5 to 0.6 in the second year; calculated from data in Berry, 1978). Blue mussels *(M. edulis)* from several populations in southwest England, including the Lynher estuary, also exhibit a comparatively low reproductive effort, although growth is relatively slow (Bayne and Worrall, 1980; Bayne et al., 1983).

Of particular interest is recent evidence that reproductive effort is variable between populations within a relatively small geographical region, whereas other quantities relating to reproductive strategy are more conservative (Bayne et al., 1983). These authors have suggested that reproductive effort is negatively correlated with the degree of stress, which is consistent with some theoretical arguments (Goodman, 1979). It may not be possible to generalise, however, since there is a body of experimental data from a variety of organisms which demonstrates the converse, i.e. enhanced reproductive effort (despite reduced fecundity) as a response to stress, especially a reduction in food ration (Calow and Woollhead, 1977; Bayne et al., 1978; Hirshfield, 1980; Thompson, 1983). An explanation for this apparent paradox may lie in the nature of the experimental regimes, which usually represent abrupt, unpredictable changes in conditions that may not elicit the same response from the animal as a consistently poor environment, in which there is the opportunity for long-term adaptation to occur. Some evidence to support this hypothesis has emerged from recent studies on *Placopecten magellanicus* (MacDonald and Thompson, unpubl.). Scallops from shallow water exhibit a greater reproductive effort than those found in deeper water, where the food supply is consistently poorer. Differences in the response to starvation may be adaptive, however. For example, Calow and Woollhead (1977) have suggested that the evolution of differences in reproductive strategy between 2 species of triclads may have resulted from differential susceptibility of hatchlings to low ration.

The curve relating residual reproductive value to age in Bellevue mussels is similar to that obtained by Bayne et al. (1983) for *Mytilus edulis* from localities in southwest England. Residual reproductive value is low in young individuals, but increases to a maximum at an intermediate age before decreasing in older members of the population. Similar data have been recorded for the Iceland scallop *Chlamys islandica* by Vahl (1981), for a primate (Schulman and Chapais, 1980) and for 2 species of snakes (Pianka and Parker, 1975). Much of

the interest in RRV has centred around the 'optimisation theory', recently restated by Goodman (1982), which predicts that maximum somatic growth should occur at an age close to the maximum RRV. Existing empirical data are, however, equivocal. Bayne et al. (1983) have provided some evidence in favour of the optimisation concept from RRV estimates in 2 populations of *M. edulis,* although in a third, the Cattewater, RRV reaches a maximum earlier than does growth rate. Data from Bellevue are similar to those from the Cattewater, but Vahl (1981) has obtained a peak for RRV which occurs in scallops much older than those in which growth is maximised. Some recent theoretical treatments have questioned the optimisation theory. For example, Caswell (1980) considers that it may apply only under very restrictive conditions and that the usefulness of a theory based on the maximisation of RRV may be limited. Ricklefs (1981) takes this argument further by regarding RRV optimisation theory as a possible constraint to the interpretation of life history strategies, e.g. in circumstances in which there is a tradeoff between growth and reproduction or survival.

In any future consideration of reproductive value, efforts should be directed towards the improvement of mortality estimates. Bayne (pers. comm.) has obtained recent data which suggest that mortality in some mussel populations in southwest England is lower in individuals of intermediate age than in younger and in older ones, i.e. a similar situation to that at Bellevue. One major difficulty lies in the assumption, implicit in the expression used to calculate RRV, that age-specific mortality is constant from year to year. The fact that very similar length-frequency distributions have been observed for a number of years in several populations of *Mytilus edulis* in Newfoundland suggests that there is some stability to the distribution, but elsewhere circumstances may be very different. Freeman and Dickie (1979) recorded considerable differences in mortality between populations of *M. edulis* a few kilometres apart. Survivorship is certainly the critical life-table parameter in this context and is probably the most difficult to measure in a marine invertebrate. The present dearth of unequivocal data for RRV may be due as much to inadequate tools (especially for the estimation of mortality) as to any deficiencies in life history theory.

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