Marine Biology 84:27–34 (1984)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Resource allocation in *Mytilus edulis* on the shore and in suspended culture

P. G. Rodhouse*, C. M. Roden, M. P. Hensey and T. H. Ryan

Shellfish Research Laboratory; Carna, County Galway, Ireland

Abstract

The annual cycle of carbon and nitrogen content of the flesh of wild and cultivated mussels (*Mytilus edulis* L.) in Killary Harbour, Ireland, was measured over two years, starting in February, 1980 and ending in November, 1981. The carbon and nitrogen contents of mussel gametes were determined and the allometry of growth of wild and cultured mussel shells was examined with respect to length, weight and organic content. The carbon and nitrogen contents of the organic fraction of the shell were determined. These data were combined with those we had previously published on growth rate, gametogenesis and the annual cycle of ash-free dry weight (AFDW) of mussels in the same locality. Estimates were made of fecundity, reproductive effort and the partitioning of carbon and nitrogen between soma, gametes and shell. In suspended culture, cumulative production after eighteen months is equal to cumulative production after six to seven years on the shore. For comparison, partitioning of carbon and nitrogen resources between soma, shell and gonad is estimated when total cumulative production by wild and cultivated mussels is approximately equal. Differences in resource allocation are considerable. Wild mussels allocate some 57% of their carbon budget and 52% of their nitrogen budget to gamete output. In culture, mussels allocate only 22% of their carbon budget and 19% of their nitrogen budget to gamete output. It is concluded that in response to a higher production rate, cultivated mussels increase allocation of resources to somatic growth.

Introduction

Mussels, *Mytilus edulis,* grown in suspended culture in Killary Harbour, Ireland differ from wild mussels in having a higher rate of growth and different seasonal cycles in flesh weight and gametogenesis. Cultured mussels spawn twice each year, in early summer and late summer. Wild mussels spawn twice each year in late winter and early summer. These differences were described by Rodhouse *et al.* (1984) and were attributed to quantitative and qualitative differences in the food resource between the photic zone offshore, where cultured mussels are held, and the shore and shallow sublittoral, where wild mussels occur. Here we address the question of whether differences in growth rate between wild and cultured mussels can be explained by differences in the partitioning of carbon and nitrogen resources between somatic growth, shell growth and gametic output. We demonstrate that cultured mussels have a higher production rate, when these three components of production are considered together. Higher production rate in culture is associated with differences in resource allocation.

The relation between growth and fecundity, expressed as reproductive effort, was determined for two Canadian populations of *Mytilus edulis* by Thompson (1979). Fecundity varied from year to year, suggesting that the proportion of energy allocated to reproduction is adjusted according to the available food ration. This is in agreement with Bayne *et al.* (1978) who demonstrated reduced fecundity in mussels exposed to temperature and nutritive stress. Fecundity differences in the Canadian mussels were not necessarily accompanied by similar shifts in reproductive effort (gamete production as a percentage of total annual production), as proportionality between resource allocation for growth and reproduction may be constant. This could not be tested in that study. Reproductive effort increased with age and there was a gradual transition from growth to reproduction. Thompson (1984) presented further data for one of the Canadian populations (Bellvue, Newfoundland) and calculated production and reproductive effort, value and cost.

Bayne and Worrall (1980) compared growth and fecundity of two populations of *Mytilus edulis* in S. W.

* Present address and address for correspondence: Department of Ecology and Evolution, Division of Biological Sciences, State University of New York at Stony Brook; Stony Brook, New York 11794, USA

England, one of which was influenced by the warm water effluent from an electricity-generating station. Seasonal weight changes and fecundity were estimated by combining Gompertz growth curves, incorporating day degrees, and monthly allometric relations between shell length and dry flesh weight. Elevated temperature at a time of poor food quality caused a reduction in growth rate at the site exposed to warm water effluent. Production of gametes was also reduced at this site.

Bayne *et al.* (1983) found that *Mytilus edulis* in southern England shows considerable variability between sites with respect to egg production, reproductive effort and reproductive value and that with environmental deterioration, age-specific reproductive effort is reduced. However, there was similarity between sites, especially with respect to egg size and metabolic cost of egg production.

Sprung (1983) found that an intertidal population of *Mytilus edulis* in Helgoland had significantly smaller eggs than a subtidal population. However, the intertidal mussels reached sexual maturity at a smaller size and had a higher egg output with respect to shell length than the subtidal mussels.

Several authors have estimated the organic content of bivalve shell by acid decalcification (Hughes, 1970; Rodhouse, 1978; Griffiths and King, 1979; Ivell, 1981). Other authors (Hibbert, 1976; Shafee, 1980; Vahl, 1981) have determined the organic content of the bivalve shell by measuring loss in weight of dry shell after ignition at 500 to 540 °C for 6 to 24 h. Rodhouse (unpublished data) has shown that estimates of the organic fraction of the shell by ignition may be too high by a factor of 2.5, presumably due to partial volatilisation of the inorganic fraction (Crisp, 1971). The shell organic fraction has been shown not only to account for a small fraction of the whole shell weight, but also to account for a substantial proportion of total body energy in *Aulacomya ater* (Molina) (Griffiths and King, 1979) and of annual production in *Ostrea edulis* L. (Rodhouse, 1979). However, in *Mytilus edulis* from Newfoundland the organic fraction of the shell contributes less than 2% of the production by the mussel (Thompson, 1984).

Most authors have used energy units in bivalve production studies (see review by Bayne and Newell, 1983). A nitrogen budget involving estimates of somatic, gonad and shell production was reported for the ribbed mussel *Geukensia demissa* (Dillwyn) by Jordan and Valiela (1982). Here we measure production in terms of carbon and nitrogen. The use of carbon and nitrogen as units of biomass allows for some discrimination between structural components and energy reserves. Ansell and Sividas (1973) proposed the use of carbon/nitrogen analysis as a means of detecting stress in bivalve populations, as the ratio of these elements in *Donax vittatus* (da Costa) was found to be sensitive to changes in carbohydrate and lipid content, which is associated with accumulation and depletion of nutrient reserves.

The data presented in this paper were collected during a three-year programme of research on the production ecology of Killary Harbour.

Materials and methods

Samples of *Mytilus edulis* (L.) were collected at monthly intervals from the shore at the level of approximately 13% aerial exposure and at a depth of 5 m, from production ropes in Killary Harbour, Ireland (Rodhouse *et al.*, 1984). Sampling commenced in February, 1980 and ceased in November, 1981.

From each sample, 12 mussels were taken for determination of carbon and nitrogen content. After removal from the shell, the flesh samples were dried at 80 °C for 24 h and ground to a homogenous powder. Sub-samples of 1 to 3 mg were weighed on a Cahn electrobalance and carbon and nitrogen content determined in a Perkin-Elmer 240 A elemental analyser, with a combustion temperature of 900 °C and using acetanilide as a standard.

In May, 1982 a sample of mussels was collected from the shore and induced to spawn in the laboratory by temperature stimulus. The spermatozoa of six males and the eggs of five females were collected separately on Whatman GF/C filters and dried at 80 °C for 6 h. Carbon and nitrogen were determined as above.

In order to determine the organic composition of the shell, a sample of shells from wild and cultivated mussels was treated with concentrated hydrochloric acid to remove calcareous matter. After rinsing in distilled water, the organic residue was dried at 80 °C for 24 h and weighed. Sub-samples were combusted at 500 °C for 6 h and reweighed. Carbon and nitrogen were determined in subsamples of homogenised residue. Shell length was determined with Vernier calipers prior to decalcification.

Rodhouse *et al.* (1984) gave the fitted von Bertalanffy growth equation, incorporating day degrees, for wild mussels at the 13% aerial exposure level. This was used to estimate monthly growth in length for wild mussels over eight years. The allometric equations relating shell length to ash-free dry weight (AFDW) in the same paper were used to estimate monthly growth in AFDW over eight years. Annual somatic production of wild mussels, to age eight years, was calculated as the increase in AFDW between each June, this being the month when wild mussels have spawned for the second time and biomass is almost entirely somatic. The data for percentage of carbon and nitrogen for wild mussels were used to estimate annual carbon and nitrogen production by the soma.

The data for seasonal changes in percentage of carbon and percentage nitrogen for wild and cultured mussels were combined with data for AFDW cycles, given by Rodhouse *et al.* (1984), to estimate size-dependent AFDW and element loss associated with the early and late spawnings, for a series of standard-sized mussels. This was done by subtracting post-spawning AFDW or element content from pre-spawning AFDW or element content. Regression lines were fitted to the $\log_{10}$ transformed data relating AFDW and element loss at spawning to AFDW immediately prior to spawning. AFDW and element loss, associated with each spawning of wild mussels, was then estimated from these equations for the appropriate seasons

over the eight years for which monthly AFDW growth was estimated.

For cultured mussels the reproductive loss of AFDW, carbon and nitrogen was calculated for the modal size class at each spawning in the year after settlement (Rodhouse *et al.* 1984). It is assumed that no spawning occurs in the year of settlement. Annual somatic production was calculated between each September, this being the month when the late spawning of cultured mussels has occurred and when biomass is almost entirely somatic. Reproductive effort for wild and cultured mussels was calculated from:

$$\frac{\text{Gamete production (carbon)/spawning}}{\text{Total production (carbon)/year}}$$

and from:

$$\frac{\text{Gamete production (carbon)/year}}{\text{Total production (carbon)/year}}$$

Results

Carbon and nitrogen content of flesh

The annual cycles of percentage carbon and nitrogen for wild and cultured mussels are given in Fig. 1. The carbon profiles for each population are broadly similar, with summer peaks in July and winter minima in February/March. The early spawning of wild mussels in late winter (Rodhouse *et al.*, 1984) is associated with a large decline in percentage carbon, but the late spawning in summer in each year coincides with a small dip in the profile. Both spawning periods in cultured mussels coincide with increasing carbon content. The nitrogen profiles for wild and cultured mussels are poorly defined. As might be expected there is a tendency for nitrogen to decline with increasing carbon in both populations. No trend is consistently associated with spawning. Both wild and cultured mussels display similar profiles of C:N ratio (Fig. 2) with a summer peak in July/August and a winter minimum in January.

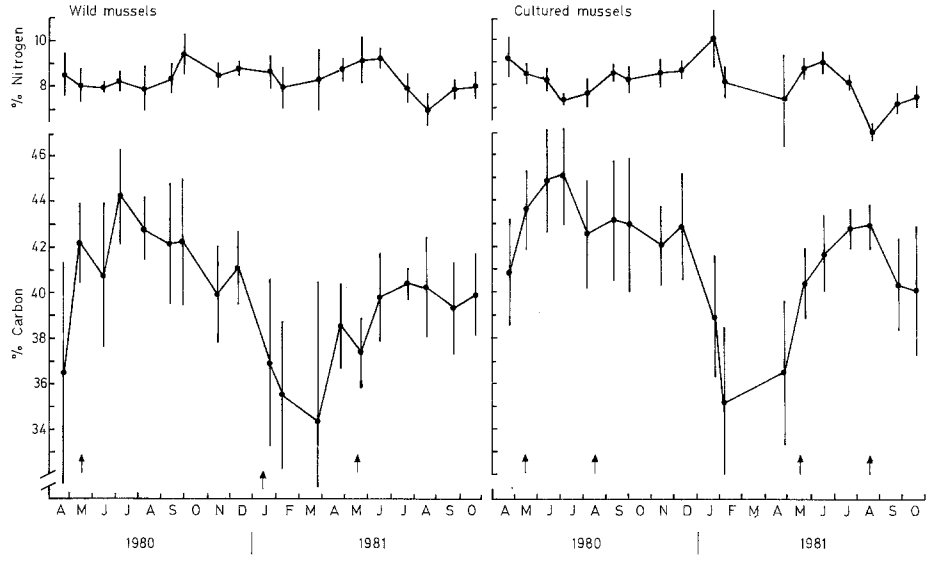

Fig. 1. *Mytilus edulis:* Annual cycle of carbon and nitrogen content of flesh (±SD) in wild and cultured mussels (onset of spawning events marked by arrows)

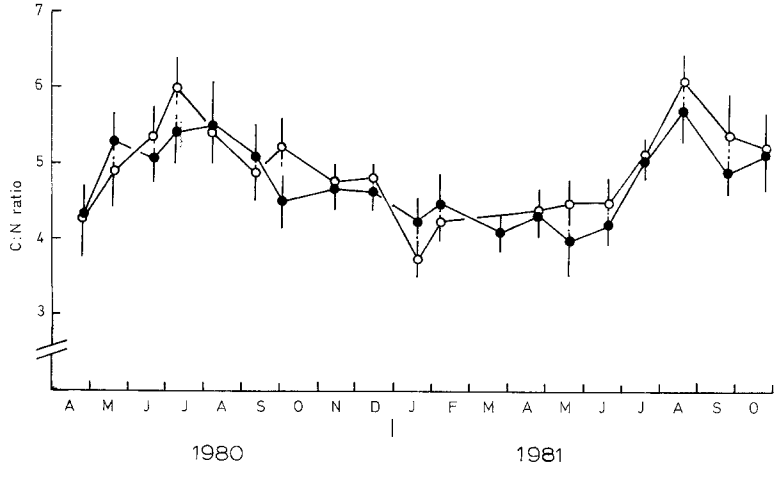

Fig. 2. *Mytilus edulis:* Annual cycle of C:N ratio (±SD). Wild mussels: ●; cultured mussels: ○

Carbon and nitrogen content of gametes

Spermatozoa of wild mussels had a carbon content of 20.57 ± 4.25% and a nitrogen content of 7.51 ± 3.24%, giving a C:N ratio of 2.74. Eggs of wild mussels had a carbon content of 39.52 ± 1.94% and a nitrogen content of 10.63 ± 0.93%, giving a C:N ratio of 3.72.

Shell allometry and carbon:nitrogen content

Dry shell weight (S_d) of wild and cultivated mussels is plotted with shell length in Fig. 3. Allometric equations were determined by linear regression analysis with $\log_{10}$ transformed data and used to calculate lines of best fit. The equation for wild mussel shell was:

$$\log_{10} S_d = -4.0639 + 2.9039 \log_{10} l \ (r = 0.995 \text{ for } 32 \text{ d.f.}),$$

and for cultured mussel shell it was:

$$\log_{10} S_d = -4.8448 + 3.1484 \log_{10} l \ (r = 0.978 \text{ for } 32 \text{ d.f.}).$$

Covariance analyses showed that there was a significant ($P < 0.05$) difference between the mean weights of wild and cultivated mussel shells after adjustment for differences in mean length, with cultured mussels having lighter shells.

Ash-free dry weight of the organic component of shells (S_o) of wild and cultured mussels is plotted with shell length in Fig. 3. Allometric equations were determined by linear regression analysis with $\log_{10}$ transformed data and used to calculate lines of best fit. The equation for shells of wild mussels was:

$$\log_{10} S_o = -6.0090 + 2.9752 \log_{10} l \ (r = 0.9971 \text{ for } 14 \text{ d.f.}),$$

and the equation for shells of cultured mussels was:

$$\log_{10} S_o = -5.5753 + 2.5727 \log_{10} l \ (r = 0.9617 \text{ for } 14 \text{ d.f.})$$

Covariance analysis showed that there was a significant ($P < 0.05$) difference between the mean organic weights of wild and cultivated mussel shells, after adjustment for differences in mean length, with cultured mussels having the lighter organic fraction.

The ash content of the shell residue after acid treatment was 16.42 ± 9.77% for wild mussels and 1.81 ± 0.47% for cultured mussels. The carbon content of the shell residue after acid treatment was 45.92 ± 2.75% and the nitrogen content was 14.34 ± 0.85% or 54.9% carbon and 17.16% nitrogen in the ash-free residue. The high nitrogen level of the organic fraction of the shell is consistent with the fact that the periostracum, ligament and conchiolin are largely protein (Wilbur, 1964).

Fecundity and reproductive effort

In all cases the regression of $\log_{10}$ AFDW and element loss at spawning on $\log_{10}$ AFDW immediately prior to spawning was significant ($P < 0.05$). The regression equations, after detransformation are given in Table 1. These can be used to predict fecundity in terms of AFDW, carbon and nitrogen from pre-spawning AFDW.

Reproductive effort of wild mussels at the early spawning is positively age- and weight-dependent, while at the late spawning it is slightly negatively age- and weight-dependent (Figs. 4 and 5). Reproductive effort of cultured mussels at each spawning and total annual reproductive effort is indicated in Figs. 4 and 5. Cultured mussels have a similar reproductive effort to wild mussels of the same age, but they are much larger than wild mussels and have a lower reproductive effort than wild mussels of the same weight at each spawning.

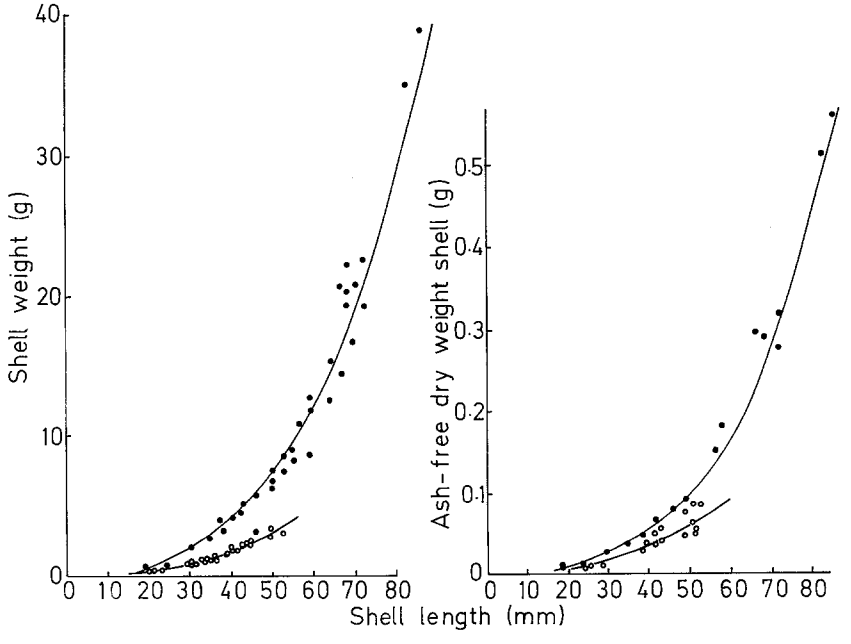

Fig. 3. *Mytilus edulis:* Relations between shell length, dry shell weight and shell organic fraction in wild and cultured mussels. Wild mussels: ●; cultured mussels: ○

Table 1. *Mytilus edulis.* Weight losses associated with spawning in wild and cultivated mussels. G = ash-free dry weight loss (mg); G_C = carbon weight loss (mg); G_N = nitrogen weight loss (mg); W = AFDW before spawning (g)

Wild mussels		
1st spawning 1981	$G = 468.2W^{1.2253}$	($r = 0.9998$; $n = 5$)
2nd spawning 1980	$G = 317.9W^{1.1947}$	($r = 0.9915$; $n = 5$)
2nd spawning 1981	$G = 238.2W^{0.8355}$	($r = 0.9997$; $n = 5$)
1st spawning 1981	$C_C = 227.4W^{1.0856}$	($r = 0.9999$; $n = 5$)
2nd spawning 1980	$G_C = 137.4W^{1.1136}$	($r = 0.9912$; $n = 5$)
2nd spawning 1981	$G_C = 108.1W^{0.8349}$	($r = 0.9998$; $n = 5$)
1st spawning 1981	$G_N = 44.7W^{1.1844}$	($r = 0.9998$; $n = 5$)
2nd spawning 1980	$G_N = 31.1W^{1.1690}$	($r = 0.9907$; $n = 5$)
2nd spawning 1981	$G_N = 23.3W^{0.8233}$	($r = 0.9997$; $n = 5$)
Cultured mussels		
1st spawning 1980	$G = 123.0W^{0.4392}$	($r = 0.9978$; $n = 3$)
1st spawning 1981	$G = 79.1W^{0.4985}$	($r = 0.9785$; $n = 3$)
2nd spawning 1980	$G = 371.0W^{0.7865}$	($r = 0.9991$; $n = 4$)
2nd spawning 1981	$G = 392.5W^{1.2038}$	($r = 0.9999$; $n = 4$)
1st spawning 1980	$G_C = 45.2W^{0.3528}$	($r = 0.9979$; $n = 3$)
1st spawning 1981	$G_C = 29.8W^{0.4316}$	($r = 0.9979$; $n = 3$)
2nd spawning 1980	$G_C = 154.4W^{0.7555}$	($r = 0.9986$; $n = 4$)
2nd spawning 1981	$G_C = 196.3W^{1.1803}$	($r = 0.9998$; $n = 4$)
1st spawning 1980	$G_N = 17.4W^{0.5030}$	($r = 0.9752$; $n = 3$)
1st spawning 1981	$G_N = 18.2W^{0.7170}$	($r = 0.9973$; $n = 3$)
2nd spawning 1980	$G_N = 23.0W^{0.6878}$	($r = 0.9966$; $n = 4$)
2ns spawning 1981	$G_N = 26.4W^{1.2343}$	($r = 0.9999$; $n = 4$)

Table 2. *Mytilus edulis.* Apparent C:N ratio of spawn, based on data in Table 1

	Shell length (mm)				
	20	30	40	50	60
Wild mussels					
1st spawning 1981	7.6	6.6	5.9	5.5	5.2
2nd spawning 1980	5.2	4.8	4.7	4.5	4.4
2nd spawning 1981	4.5	4.5	4.5	4.6	4.6
Cultivated mussels					
1st spawning 1980	3.7	3.1	2.8		
1st spawning 1981	3.7	2.5	1.9		
2nd spawning 1980	5.7	6.2	6.5	6.8	
2nd spawning 1981	8.8	8.2	7.7	7.4	

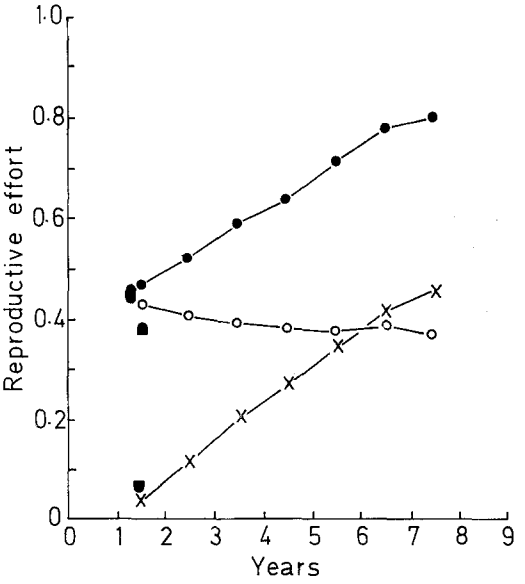

Fig. 4. *Mytilus edulis:* Reproductive effort of wild mussels as a function of age (early spawning: ×; late spawning: ○; combined: ●). Reproductive effort of cultured mussels during year following settlement is indicated (early spawning: ▼ ; late spawning: ▲ ; combined: ⬮)

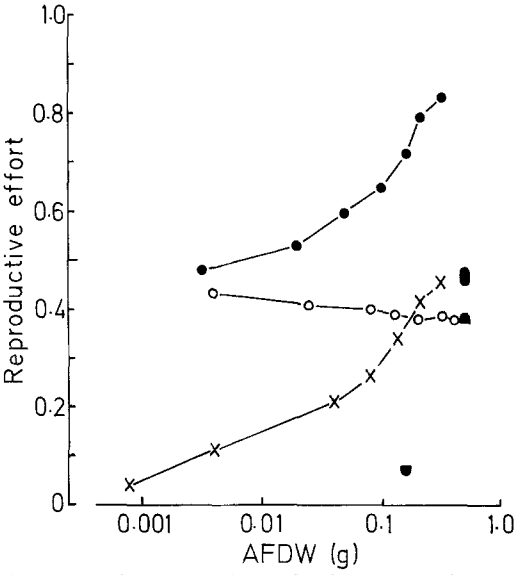

Fig. 5. *Mytilus edulis:* Reproductive effort of wild mussels as a function of AFDW (early spawning: ×; late spawning: ○; combined: ●). Reproductive effort of cultured mussels during year following settlement is indicated (early spawning: ▼ ; late spawning: ▲ ; combined: ⬮)

The data in Table 1 were used to calculate the apparent C:N ratio of gametes from a range of size classes, for each spawning of wild and cultured mussels (Table 2). This ratio represents a population average for males and females. The apparent C:N ratio of gametes from the early spawning of wild mussels in 1981, and the late spawning of cultured mussels in 1980 and 1981, are somewhat higher than expected in view of measured C:N ratios of 2.74 for wild mussel sperm and 3.72 for wild mussel eggs. This suggests that either there are differences in elemental composition of gametes at these spawnings or the occurrence of carbon losses during these periods are not associated with release of gonad products, but due to metabolism of energy reserves. Winter depletion of energy reserves (glycogen) was described for populations of mussels elsewhere (De Zwaan and Zandee, 1972) and it appears from the AFDW and C:N ratio data, for cultured mussels from Killary Harbour, that late summer, autumn and winter are periods of energy reserve depletion for mussels growing on ropes.

The late spawning of wild mussels in 1980 and 1981, and the early spawning of cultured mussels in each year both occur in May/June. Apparent C:N ratios for gametes released at this time are closer to expected values, suggesting little or no depletion of energy reserves at this time. There is some evidence of accumulation of energy reserves in cultured mussels as there was a lower than expected, apparent C:N ratio in 1981. Accumulation of energy reserves, concurrent with gametogenesis, was demonstrated by Lowe *et al.* (1982). If this continues during spawning it will result in an increase in flesh C:N ratio, thus depressing the apparent C:N ratio of gametes, calculated from changes in elemental composition of adult flesh.

Carbon and nitrogen allocation

In order to compare the relative capacity for production between wild and cultured mussels, total annual production (somatic, gonad and shell organic fraction) was calculated for an average individual at the 13% exposure level on the shore and for an average individual grown in suspended culture. Cumulative total annual production, in terms of carbon, is shown in Fig. 6. On the average it takes 6 to 7 years on the shore, at the 13% exposure level, to attain the production achieved by cultured mussels by the time they are harvested at 18 months after settlement. Total production rate by mussels grown on ropes is thus approximately four times that of the wild mussels on the shore.

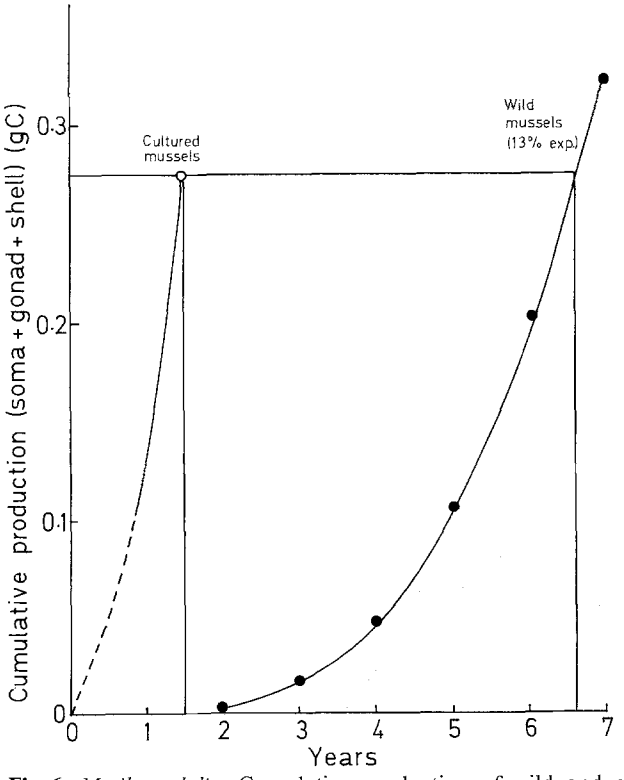

Fig. 6. *Mytilus edulis:* Cumulative production of wild and cultured mussels

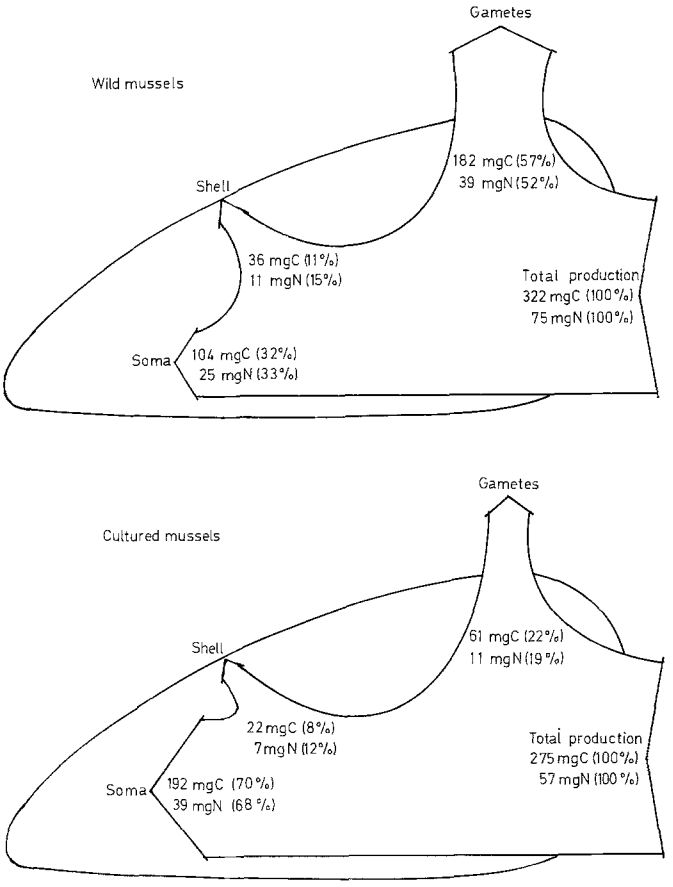

Fig. 7. *Mytilus edulis:* Allocation of carbon and nitrogen in wild and cultured mussels

A comparison of the way carbon and nitrogen resources have been partitioned between soma, gonad and shell by wild mussels on the shore at the 13% exposure level and cultured mussels grown on ropes, once total cumulative production is approximately equal, is given in Fig. 7. On the shore, after 6 to 7 years, larger amounts of carbon and nitrogen have been diverted to gonad than soma. A slightly larger percentage of nitrogen than carbon is associated with shell production. At 18 months after settlement, somatic production of cultured mussels accounts for more than three times gonad production in terms of both carbon and nitrogen. Shell production in terms of the percentage of each element is somewhat less in cultured mussels but the difference is not large.

Discussion

Mussels grown in suspended culture in Killary Harbour receive a superior food resource and grow faster than wild mussels on the shore (Rodhouse *et al.*, 1984). This enhanced growth rate in culture is reflected in increased production of soma, gonad and shell. Differences in production between wild and cultivated mussels are apparently associated with differences in allocation of the carbon and nitrogen resource between somatic growth, gonad output and shell deposition.

Differences between wild and cultured mussels in their allocation of resources to gametes are complex, largely because there are two annual spawning events, with differences within each population, between each spawning. The equations in Table 1 relating fecundity to pre-spawning weight show that in wild mussels the weight exponent for fecundity is fairly constant with spawning time and approximates 1.0. Bayne *et al.* (1983) found a similar exponent for mussels from south-west England and south Wales although other authors [reviewed by Sprung (1983)] have reported somewhat higher values. When fecundity is measured in terms of AFDW or carbon, the intercept in the equations for wild mussels is higher for the early spawning, however, this difference is diminished when fecundity is measured in terms of nitrogen. These differences give rise to differences in the apparent C:N ratio of gametes. It is possible that differences exist between the elemental content of gametes at the early and late spawnings. Bricelj and Malouf (1980) showed that in *Mercenaria mercenaria* from Great South Bay, New York, which have two spawnings per year, the eggs produced during the late spawning event are smaller than those produced during the early spawning. Egg size in *Mytilus edulis* may also be related to position on the shore relative to tidal height (Sprung, 1983). However, in another study Bayne *et al.* (1983) showed that the eggs of *M. edulis* are remarkably consistent with respect to size over a wide range of environmental conditions. An alternative explanation for differences in apparent C:N ratio of gametes may be that they are due to carbon depletion in the adult wild mussels, concurrent with the early spawning. If this is the case, then measurement of fecundity by indirect inference from carbon or weight changes in parent mussels would be confounded. Nitrogen loss may thus provide a better indirect measure of fecundity. Nitrogen (protein) depletion not associated with spawning may occur during late winter (Dare and Edwards, 1975) when wild mussels in Killary Harbour are spawning, but with glycogen as the major energy reserve, errors associated with metabolic depletion of nitrogen will be relatively small unless there is undue nutritive and temperature stress.

The equations in Table 1 show that in cultured mussels the weight exponent for fecundity is generally less than for wild mussels and differs between the early and late spawning. When fecundity is measured in terms of AFDW or carbon, the intercept in the equations is higher in the late spawning than in the early spawning, but this difference is much reduced when fecundity is measured in terms of nitrogen. As for wild mussels this may be due to differences in the elemental composition of the gametes or to depletion of carbon reserves by the parents, concurrent with the late spawning in August/September, when the food resource in Killary Harbour starts to decline for mussels cultured off the bottom (Rodhouse *et al.*, 1984).

Reproductive effort is expressed in terms of the carbon budget. This may overestimate reproductive effort if carbon is coincidently lost in non-gametic form during the early spawning. However, these non-gametic carbon losses may be associated with the metabolic maintenance of gametes and can perhaps be legitimately included as part of the reproductive effort (see Calow, 1979). Reproductive effort of wild mussels at the early spawning is markedly size-dependent, and by inference age-dependent, whilst at the late spawning reproductive effort is slightly negatively size-dependent and relatively high for small young mussels. The presence of a late spawning results in total annual reproductive effort being considerably higher in small mussels by comparison with populations in which there is a single annual spawning (Bayne *et al.*, 1983), whilst in older mussels (ca 8 years) reproductive effort converges with that reported by these authors for mussels living in non-stressed environments. We conclude that at the early spawning small wild mussels have little energy available for gametic output. They are unable to gain weight during the previous autumn (Rodhouse *et al.*, 1984) and they have had a relatively high metabolic rate and thus high demand on energy reserves by comparison with larger individuals during the winter period of reduced food resource. Conversely during the summer months, when the food resource is in excess of the maintenance requirement, small mussels are able to direct a relatively high fraction of their resources to gametogenesis. Reproductive effort for cultured mussels, shown in Figs. 4 and 5, was calculated for the modal size for the cohort. Effort is higher at the late spawning when the mussels are larger.

In order to compare the strategies adopted by wild and cultured mussels for partitioning resources between soma, gonad and shell, we drew the comparison at the point where total cumulative production is approximately equal. i.e. at 18 months for cultured mussels and six years for wild mussels. At that time wild mussels have allocated a considerable percentage of their accumulated reserve (57% C; 52% N) to gonad by comparison with cultured mussels (22% C; 19% N to gonad).

When grown in suspended culture, mussels produce a considerably lighter shell than when growing wild on the shore. This difference is due to differences in both the organic and inorganic components of the shell. However, Fig. 7 shows that at the time of approximately equal cumulative production, a similar small percentage of the carbon and nitrogen resource has been allocated to shell production in wild and cultivated mussels.

The allocation of resources between somatic growth and gametic production is of fundamental importance within the context of life-history theory. Goodman (1979) predicted on theoretical grounds that when the older breeding age classes of a species are less affected by environmental change than younger classes, or when potential adult survival is less affected than potential survival of young, then fitness is maximised by increasing reproductive effort with environmental amelioration and decreasing reproductive effort with environmental deterioration. Bayne *et al.* (1983) found that under conditions of environmental stress, defined as reduced scope for growth (Warren and Davis, 1967), *Mytilus edulis* reduces reproductive effort. However, experimental studies of

other organisms show that an increase in reproductive effort may occur in response to stress (Calow and Woollhead, 1977; Hirshfield, 1980; Thompson, 1983). Thompson (1984) suggested that this response may arise in experiments where conditions are changed abruptly and unpredictably, and the results may not reflect the response which would be elicited in a consistently poor environment. Our data suggest that in the artificial, but long-term, conditions of suspended culture in Killary Harbour, *M. edulis* apparently reduces the allocation of resources to gametic production in the presence of environmental amelioration.

Acknowledgements. We thank Professor P. O'Ceidigh and Dr. J. P. Mercer for providing facilities at the Shellfish Research Laboratory. Mr. J. O'Neill, Mr. T. MacMahon, Mr. T. Redmond and Mr. M. Rowley contributed to field and laboratory work and Mr. D. Brown contributed technical assistance on numerous occasions. Mrs. D. Rodhouse helped with preparation of the manuscript and Mrs. R. Sickles prepared the typescript. Dr. R.I.E. Newell and Dr. R. J. Thompson helpfully criticised the manuscript. The Killary Harbour project was funded by the National Board for Science and Technology (Ireland) and Beirtreach Teoranta. Contribution No. 238 from School of Marine Science, University College, Galway.

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Date of final manuscript acceptance: August 22, 1984.
Communicated by M. Shick, Orono