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FOOD RESOURCE, GAMETOGENESIS AND GROWTH OF *MYTILUS EDULIS* ON THE SHORE AND IN SUSPENDED CULTURE: KILLARY HARBOUR, IRELAND

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(Figs. 1–11)

Mussels, *Mytilus edulis* L. grow on the shore and are cultured on ropes in Killary Harbour, a fjordic inlet on the Irish west coast. The food resource available to cultured mussels differs from that available to wild mussels on the shore. Although phytoplankton densities as estimated from chlorophyll *a* concentrations are similar, the shore environment in the inner part of the inlet is characterized by high mean POC concentrations. This is because of the presence of variable amounts of allochthonous detrital carbon.

The annual cycles of flesh weight and ash content of wild and cultivated mussels were followed over two years. These cycles were related to the reproductive cycle observed by taking histological samples of mussel gonad, by plankton sampling for larvae and by monitoring larval settlement. Shell growth was measured in wild mussels by reading seasonal growth patterns on sectioned shells and in cultured mussels by following progress of the modal shell length of cohorts on ropes.

Wild mussels have a partial spawning in early spring and spawn completely in the summer. Cultured mussels spawn twice during the summer, in the year following settlement. Growth rate of wild mussels decreases with increasing aerial exposure. The fastest growing mussels, at 0% exposure, take about 6 years to attain the length attained by the mode of the cultured mussels after 18 months, when they are harvested.

We conclude that wild mussels utilize a mix of phytoplankton and detritus as food during the summer and that large wild mussels can use detritus during the autumn and early winter for an increase in flesh weight and gametogenesis. This results in a partial spawning restricted to large individuals in the spring. Cultured mussels are mainly dependent on phytoplankton for food. This supports fast growth and two spawning bouts during the summer, but flesh weight declines once phytoplankton densities fall in the autumn.

INTRODUCTION

Culture of mussels, *Mytilus edulis* L., on ropes suspended from rafts or long lines is a well-established industry in several countries (Mason, 1976; Lutz, 1980). In Ireland, the industry centres on Killary Harbour, a fjordic inlet on the west coast (Fig. 1). A dense population of mussels occurs on the shores of the inner part of the inlet, and the experience of commercial growers has shown that larval settlement is heaviest here. Ropes are seeded here during peak settlement periods

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in early and mid-summer and then moved to rafts and long lines in the outer part of the inlet, or to other coastal sites for growing to commercial size (40–50 mm shell length). Harvest takes place from November to January, after approximately 18 months growth.

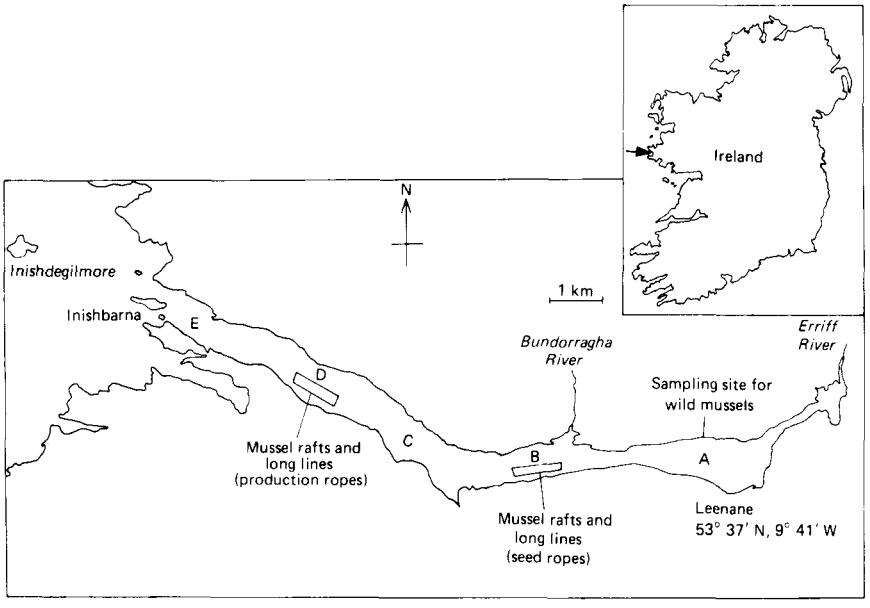

Fig. 1. Killary Harbour: sampling stations and the positions of rafts and long lines.

In this paper we compare growth rate, allometry, the annual cycle of flesh weight and the gametogenic cycle of wild mussels and those grown in suspended culture. Considerable differences exist, and these are examined with reference to the food resource available to wild and cultured mussels.

The relations between food quantity, temperature and scope for growth in *M. edulis* have been described by Thompson & Bayne (1974), Widdows (1978*a*, *b*) and Bayne & Worrall (1980). The effect of food concentration on growth has been measured in mussels by Winter & Langton (1976). Newell *et al.* (1982) show that quantitative and temporal differences between habitats, in the energy content of the mussels' food supply, have a marked influence on the timing of the gametogenic cycle.

Qualitative aspects of bivalve food are less well understood. Russell-Hunter (1970) and Mann (1972) discuss C:N ratio and potential nutritional value of detritus in freshwater and marine environments. Blegvad (1914), Coe & Fox (1942; 1944), Fox & Coe (1943) and Fraga & Vives (1960), cited by Seed (1976), have concluded that organic detritus supplies a large part of the diet of mussels. However, experiments with artificially prepared detritus fed to *Argopecten irradians* (Say) (Kirby-Smith, 1976) and *M. edulis* (Williams, 1981) were inconclusive. Widdow's Feith & Worrall (1979) found that in the Lynher Estuary, in south-west England, phytoplankton concentrations only exceed the mainten-

ance ration for *M. edulis* in June to August, and suggest that detritus or bacteria contribute to nutrition. Kiørboe, Møhlenberg & Nøhr (1981) concluded that the organic fraction of resuspended bottom material contributes to the growth of *M. edulis*. Stephenson & Lyon (1982) have shown, by stable carbon isotope analysis, that detrital carbon of terrestrial origin contributes to the nutrition of the venerid bivalve *Chione stutchberyi*. Stuart, Field & Newell (1982) have demonstrated that the mussel *Aulacomya ater* (Molina) absorbs kelp debris with an efficiency of about 50%, and Stuart (1982) found that this species was able to maintain positive scope for growth when fed kelp debris at concentrations > 1 mg . l^{-1}.

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

Table 1. *Depths sampled at each station for chlorophyll* a, *POC and PON*

Station	Depth sampled (m)	Station	Depth sampled (m)
A	0, 4	D	0, 5, 10, 15
B	0, 5, 10	E	0, 5, 10, 15
C	0, 5, 10		

MATERIALS AND METHODS

Food availability

At approximately two-week intervals between March 1980 and January 1982, 6l water samples were collected with a Van Dorn water sampler at each of five stations along the length of Killary Harbour (Fig. 1). The depths sampled at each station are given in Table 1. For particulate organic carbon and nitrogen (POC and PON) analysis, 1l aliquots were concentrated on pre-combusted GF/C filters. These were frozen at −20 °C until ready for assay with a Perkin–Elmer 240A elemental analyser. For chlorophyll *a* analysis 1–4l aliquots were concentrated on GF/C filters and assayed according to Strickland & Parsons (1972).

Phytoplankton samples were collected at two-week intervals with the Van Dorn water sampler at station D in 1981 and preserved with neutral formalin. Samples (25 ml) were sedimented and examined with an inverted microscope. Cell counts were made either by counting diameter strips at × 100 magnification or by counting half the entire chamber.

Suspended particulate inorganic matter (PIM) was determined monthly, between September 1981 and July 1982, for water samples collected from 0·5 m off the bottom at station A, and at a depth of 5 m at station D. One litre of sea water was concentrated on the pre-combusted, pre-weighed GF/C filters, washed with distilled water to remove salt and combusted for 4 h at 500 °C before weighing.

Allometry and histology

Mussel samples were collected at monthly intervals from the shore, at approximately the 13% aerial exposure level and at a depth of 5 m, from production ropes. Sampling commenced in February 1980 and ended in November 1981. Approximately thirty mussels from each sample, covering the size range present, were selected for determining allometric relations. Shell length was measured, after which the flesh was dissected out, dried for 24 h at 80 °C, weighed, combusted for 6 h at 500 °C and re-weighed. Samples were cooled in a desiccator prior to each weighing.

From a further twenty mussels from each sample, a small piece of tissue was excised from the mantle, for histological examination. These samples were fixed in Davidson's fixative and dehydrated in an ascending alcohol series for wax embedding, sectioning, staining with haematoxylin–eosin and mounting.

Gamete volume fraction (GVF) was determined by stereology (Bayne *et al.* 1978). This measures reproductive condition in terms of the proportion of mantle tissue composed of developing or ripe gametes.

Morphological condition of the gonad was classified according to a scheme similar to that proposed by Lubet (1959), and each stage assigned a rank. Stage 0, the resting stage, was ranked 0 and has no trace of sexuality. Stages I and II ranked 1 and 2 are developing stages, and stage III A ranked 3 is morphologically ripe. No stage defined as spawning was used as this was considered too subjective. Where there was evidence of spawning in a sample, this was assigned to stage III A. Stage III B ranked 1 is the spent phase and stage III C, ranked 2 is a recovery phase, present when a second spawning is to take place. A population gonad index (Seed, 1976) was calculated from $\Sigma(100\,gn)/N$ where g is a rank number from 0 to 3, n is the number of mussels assigned to a rank and N is the sample size.

Larval abundance and settlement

Quantitative zooplankton samples were collected at stations B, D and E at two-week intervals between February 1981 and January 1982, using a 1 m diameter zooplankton ring net with a 90 μm mesh. The net was towed obliquely from the surface. Estimates of the volume filtered (2–10 m^3) were made with a digital flowmeter (General Oceanics mod. no. 2030) mounted in the mouth of the net. The samples were preserved with neutral formalin and counted after subsampling. Results were recorded as numbers m^{-2}. Settlement of mussel larvae was monitored, in 1980 and 1981, on 0·3 m lengths of coir rope suspended 3 m below the surface from the rafts at station B. The ropes were replaced at weekly intervals and the spat counted under a binocular microscope.

Growth

In April 1981 the wild population of mussels on the north shore, opposite station A, was sampled from three zones corresponding to approximately 33 %, 13 % and 0 % aerial exposure. Shell lengths of mussels covering the size range present were measured, sectioned and assigned an age by reading the annual growth patterns, described for *M. edulis* by Lutz (1976).

Shell growth of cultivated mussels on ropes was followed by sampling a production raft and long line. Between April 1981 and March 1982 monthly samples of mussels were taken by clearing a 300 mm length from three ropes at a depth of 5 m. The samples were taken at intervals along the raft, or long line axis, parallel to the tidal stream. Percentage size frequency of the population, which derived from a single settlement, was determined after shell measurements were made on a sub-sample.

RESULTS

Food availability

Mean chlorophyll *a* data over the depth range sampled are given in Fig. 2 for each station. No data were collected for stations B and D during 1980. Minimal values occur in winter (January). Values increase to a maximum during the spring bloom in April. The summer is characterized by a series of peaks which start to decline in October. Mean values, over the time period that samples were taken, were very similar at each station. There is no significant ($P > 0{\cdot}10$) product–moment correlation between distance from the mouth of Killary Harbour (Fig. 1) and mean chlorophyll *a*.

POC and PON data were collected during 1981. Mean POC and C:N ratio data, over the depth range sampled are given for each station in Fig. 3. Stations A and B showed highly variable values for POC. C:N ratio was relatively high (> 10) during the winter (November–March) and is variable but generally lower (< 10) during the rest of the year. POC at stations D and E shows little variation through the year. C:N ratios are relatively high during the winter and are lower

and remain relatively stable during the rest of the year. Station C is intermediate between the inner and the outer stations with respect to POC and C:N ratio. The annual mean POC values at each station increase towards the head of the fjord so that there is a significant ($P < 0{\cdot}05$) correlation between distance from Inishbarna and POC concentration. At stations D and E between April and October there is significant ($P < 0{\cdot}05$) positive correlation between POC and chlorophyll *a*. At stations A and B, during the same period, no significant ($P > 0{\cdot}50$) correlation exists between POC and chlorophyll *a*.

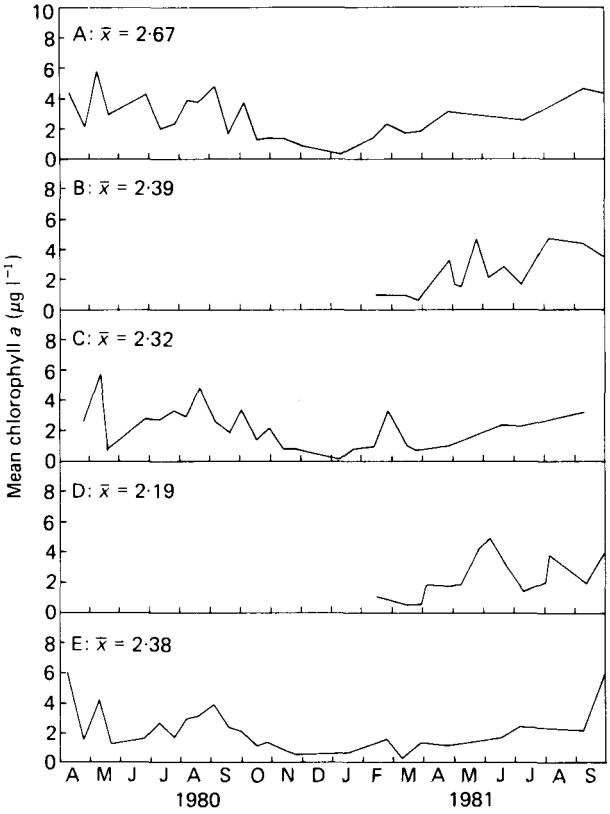

Fig. 2. Killary Harbour: mean chlorophyll *a* concentration at each station.

Until the spring bloom the phytoplankton consisted of a number of diatom species with some flagellates (e.g. *Eutreptiella* sp.) and occasional dinoflagellates. During the spring bloom in April the diatom *Thalassiosira rotula* Meun. was overwhelmingly dominant, with other diatoms increasing in number. In May the phytoplankton was dominated by *Thalassiosira* sp., *Skeletonema costatum* (Greville) Cleve and *Nitzschia delicatissima* Cleve. By June these species declined and the dominant was the coccolithophorid flagellate *Emiliana huxleyi* (Lohm.) Hay with a number of large dinoflagellates, e.g. *Ceratium fusus* (Ehrenb.) Dujard and *Scrippsiella* sp. By late July these declined and were replaced by diatoms,

especially *Rhizosolenia setigera* Brightw. and *Thalassionema nitzschioides* Hust. These were succeeded by other diatoms, especially *Leptocylindrus danicus* Cleve and the unusual warm-water diatom *Schroederella* sp. After October the phytoplankton was very sparse and no one species was dominant.

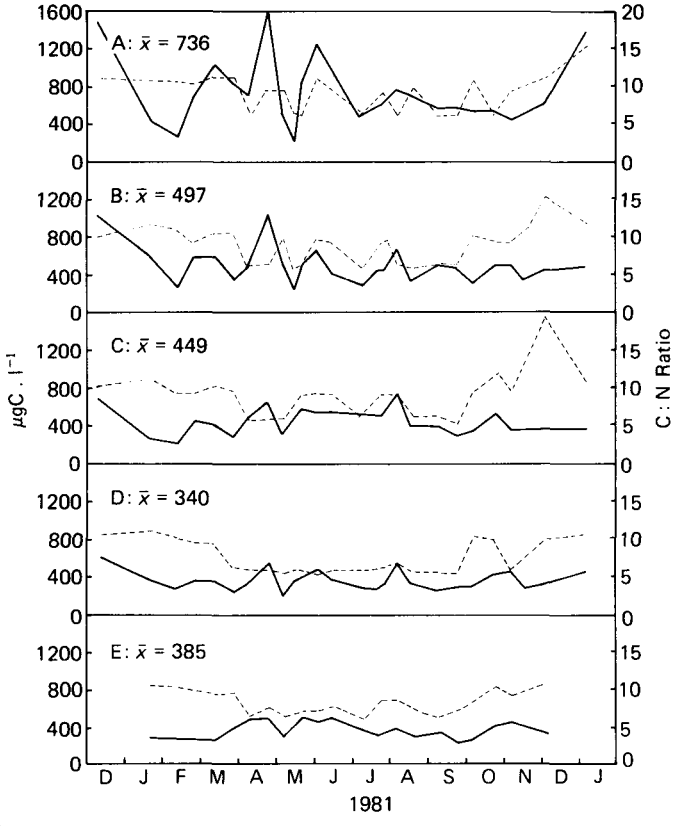

Fig. 3. Killary Harbour: mean POC (solid line) and C:N ratio (broken line) at each station.

The inorganic component of the seston showed no seasonal trend at either station sampled. At station A the mean concentration was $2{\cdot}95 \pm 2{\cdot}56$ mg . l^{-1} and at station D the mean concentration was $2{\cdot}03 \pm 1{\cdot}32$ mg . l^{-1}. The *t*-test showed that the difference was not significant ($P > 0{\cdot}20$).

Allometry and flesh weight cycle

Monthly allometric equations relating $\log_{10}$ ash-free dry flesh weight (AFDW) to $\log_{10}$ shell length (l) for wild and cultivated mussels were derived by linear regression analysis. These are given in Table 2. Analysis of covariance demonstrated significant ($P < 0{\cdot}05$) difference between the estimates of slope (b) in the allometric relationship for both wild and cultivated mussels during the seasonal cycle. The equations derived for each sample were therefore used to calculate AFDW for a series of standard-length mussels from each population. The results

Table 2. *Monthly allometric equations relating ash-free dry flesh weight (AFDW) to shell length (l) ($log_{10}AFDW = A + b\ log_{10}l$) for wild and cultured mussels with correlation coefficient (r) and sample size (N)*

Date	*A*	*b*	*r*	*N*
		Wild mussels		
7 Feb. 1980	−5·5534	2·9823	0·9578	50
18 Mar. 1980	−5·0235	2·6203	0·9102	34
22 Apr. 1980	−4·5377	2·4208	0·9463	68
13 May 1980	−4·9490	2·6887	0·9681	34
12 June 1980	−4·7670	2·6885	0·9442	42
4 July 1980	−3·9870	2·1619	0·9339	39
6 Aug. 1980	−4·3299	2·3389	0·9202	34
8 Sept. 1980	−4·0120	2·1757	0·7853	34
26 Sept. 1980	−3·9153	2·0158	0·8838	34
12 Nov. 1980	−4·9050	2·6564	0·8257	34
9 Dec. 1980	−5·8441	3·2345	0·9658	34
21 Jan. 1981	−6·0532	3·2995	0·9823	33
5 Feb. 1981	−5·9190	3·1816	0·9758	34
23 Mar. 1981	−5·5908	2·9656	0·9834	19
24 Apr. 1981	−5·2702	2·9480	0·9853	20
20 May 1981	−5·4059	3·0245	0·9784	25
16 June 1981	−5·7884	3·1745	0·9264	24
21 July 1981	−5·4562	3·0843	0·9904	25
18 Aug. 1981	−5·9456	3·3730	0·9704	25
25 Sept. 1981	−5·4623	3·0335	0·9098	25
21 Oct. 1981	−5·6444	3·1085	0·8739	25
24 Nov. 1981	−5·5650	3·0760	0·9493	25
		Cultured mussels		
12 Feb. 1980	−6·2376	3·5296	0·9689	50
11 Mar. 1980	−5·2906	2·8944	0·9631	34
24 Apr. 1980	−4·8382	2·7234	0·9658	33
15 May 1980	−4·0292	2·3480	0·9670	31
12 June 1980	−4·4516	2·5608	0·9283	43
4 July 1980	−5·1451	3·0191	0·9180	43
6 Aug. 1980	−4·6226	2·7485	0·9132	34
8 Sept. 1980	−5·7297	3·2900	0·6921	24
1 Oct. 1980	−6·1745	3·5415	0·9516	34
12 Nov. 1980	−6·0864	3·4448	0·9265	44
9 Dec. 1980	−5·9692	3·3307	0·9762	33
21 Jan. 1981	−5·8582	3·2518	0·9866	34
11 Feb. 1981	−6·4038	3·6012	0·9900	34
(March sample lost)				
23 Apr. 1981	−5·1921	2·8205	0·9783	24
20 May 1981	−5·2093	2·9680	0·9721	25
16 June 1981	−5·6511	3·3647	0·9845	23
21 July 1981	−6·3645	3·7819	0·9811	24
18 Aug. 1981	−5·7600	3·4073	0·9858	25
23 Sept. 1981	−5·4956	3·1258	0·9411	25
21 Oct. 1981	−6·3785	3·6673	0·9551	25
18 Nov. 1981	−6·1551	3·5369	0·9694	25

are plotted in Figs. 4 and 5 for wild and cultivated mussels respectively. The percentage ash content of dry flesh is also given.

There is considerable seasonal variation in AFDW in each population. The amplitude is greater in cultured mussels, so that during periods of maximum AFDW these have a considerably higher AFDW than the equivalent-sized mussels on the shore. During periods of minimum AFDW this difference remains

but is less pronounced. In both populations periods of high AFDW are associated with low ash content.

The seasonal cycle of AFDW varies with size in the wild population. Most noticeable is the gain in weight amongst the larger but not the smaller mussels during December, January and February. There is also a difference in the pattern of the seasonal cycle between the wild and cultured populations. Cultured mussels show no winter maximum and there are two summer maxima, while in the wild population there is a winter maximum and a summer maximum.

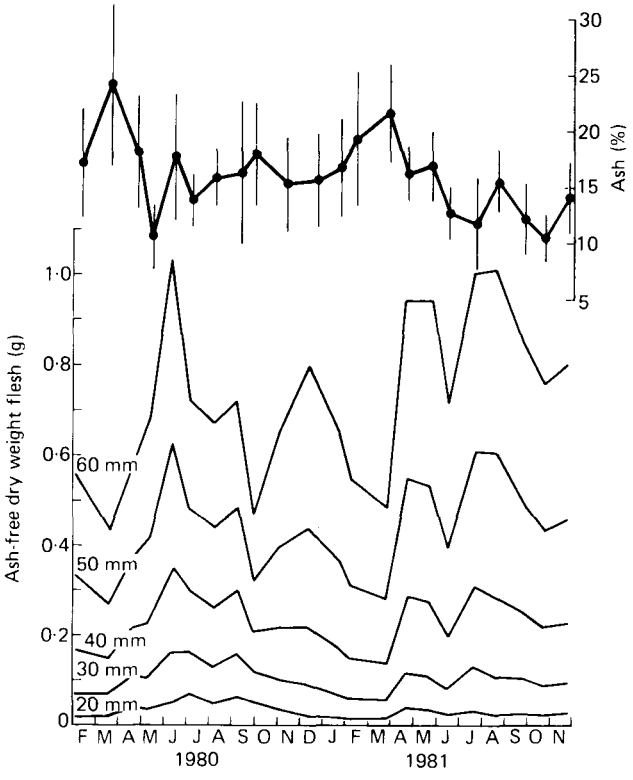

Fig. 4. *Mytilus edulis*: annual cycle of ash-free dry weight and ash content (±S.D.). Wild mussels.

Gametogenic cycle

The gametogenic cycles of wild and cultured mussels, in terms of GVF and gonad indices, are shown in Fig. 6. There is good agreement between the two methods of assessing reproductive condition. The wild population is largely in the resting and early developing phase from mid- to late-summer, followed by development through to mid-winter. In 1980 there was clear evidence of spawning in late winter and early spring in February/April. This was followed by a summer spawning in May/June and a subsequent return to the resting phase. In 1981 the gonad index showed little evidence of an early spawning, but a summer spawning at about the same time as 1980 was well marked.

In 1981 there were spring and summer maxima of larval numbers in the plankton in April and August (Fig. 7) and larvae are present throughout the year in lesser numbers. Two peaks of settlement on ropes occurred, one in May/June and the other in July, in both 1980 and 1981.

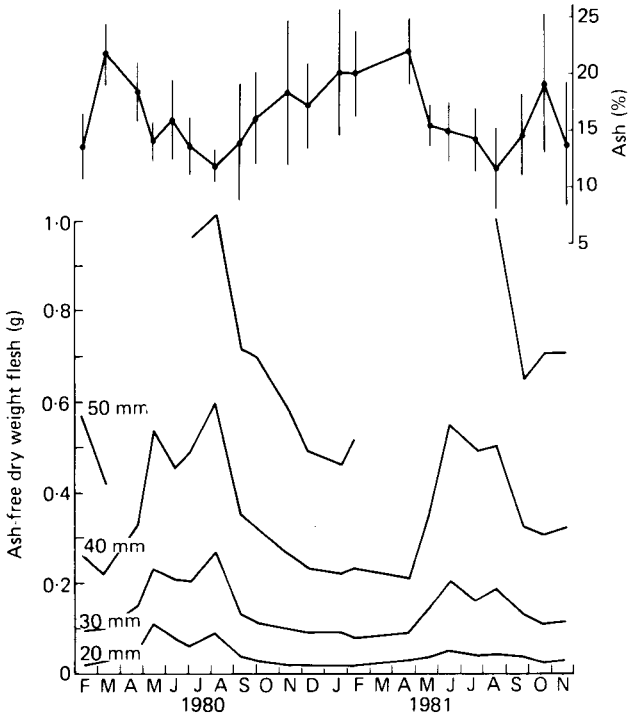

Fig. 5. *Mytilus edulis*: annual cycle of ash-free dry weight and ash content (±S.D.). Cultured mussels.

Cultured mussels which settled in 1979 began gametogenesis by the late winter of 1979/80. Two spawnings occurred in 1980 in May/June and August/September and a similar pattern was repeated in 1981 by 1980-settled mussels. A small peak of larval numbers in October/November (Fig. 7) may derive from the late, second spawning of cultivated mussels.

Mussel growth

The von Bertalanffy growth model was fitted to the data for mean length at age for shore mussels using the technique described by Ricker (1975). For 0% exposure

$l_t = 89[1 - e^{-0{\cdot}1395(t-1{\cdot}3149)}]$; for 13% exposure

$l_t = 69\ [1 - e^{-0{\cdot}1524(t-0{\cdot}9527)}]$ and for 33% exposure

$l_t = 67\ [1 - e^{-0{\cdot}0972(t+0{\cdot}4395)}]$, where l_t is shell length at time t (years). The fitted growth curves are plotted in Fig. 8. There is no evidence of the sigmoidicity in the data which has led other workers (Theisen, 1973; Bayne & Worrall, 1980) to fit the Gompertz model.

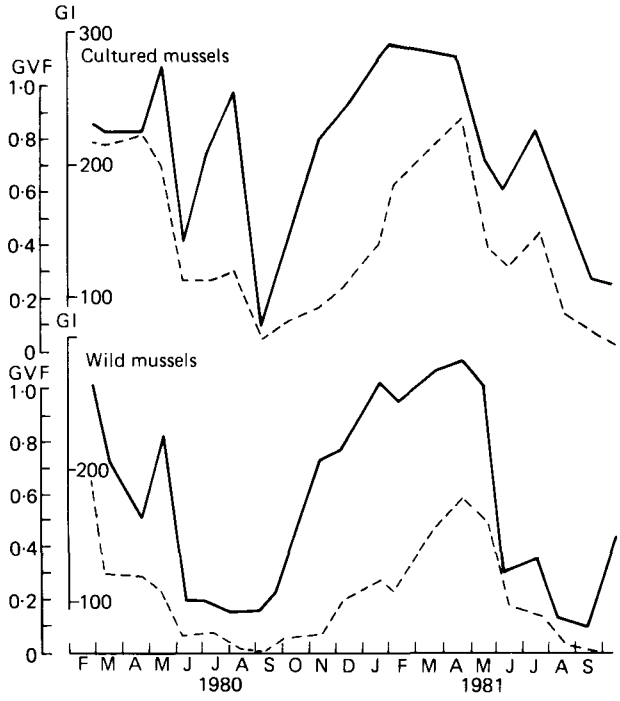

Fig. 6. *Mytilus edulis*: annual cycle of gonad volume fraction (GVF) (broken line) and gonad index (GI) (solid line). Wild and cultivated mussels.

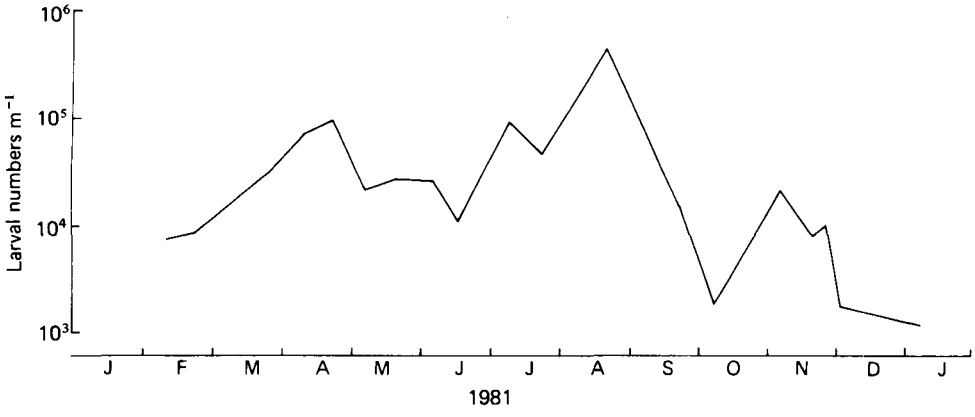

Fig. 7. *Mytilus edulis*: annual cycle of mean larval abundance in Killary Harbour in 1981.

The allometric equation relating shell length to AFDW for June 1981 (Table 2) was used to calculate AFDW from predicted shell length at yearly intervals. The resulting AFDW growth trajectories for each level of aerial exposure on the shore are given in Fig. 9. Seasonal growth in shell length was predicted by incorporating day degrees (D°) into the von Bertalanffy model, using a similar method to that described by Bayne & Worrall (1980), to incorporate D° into the

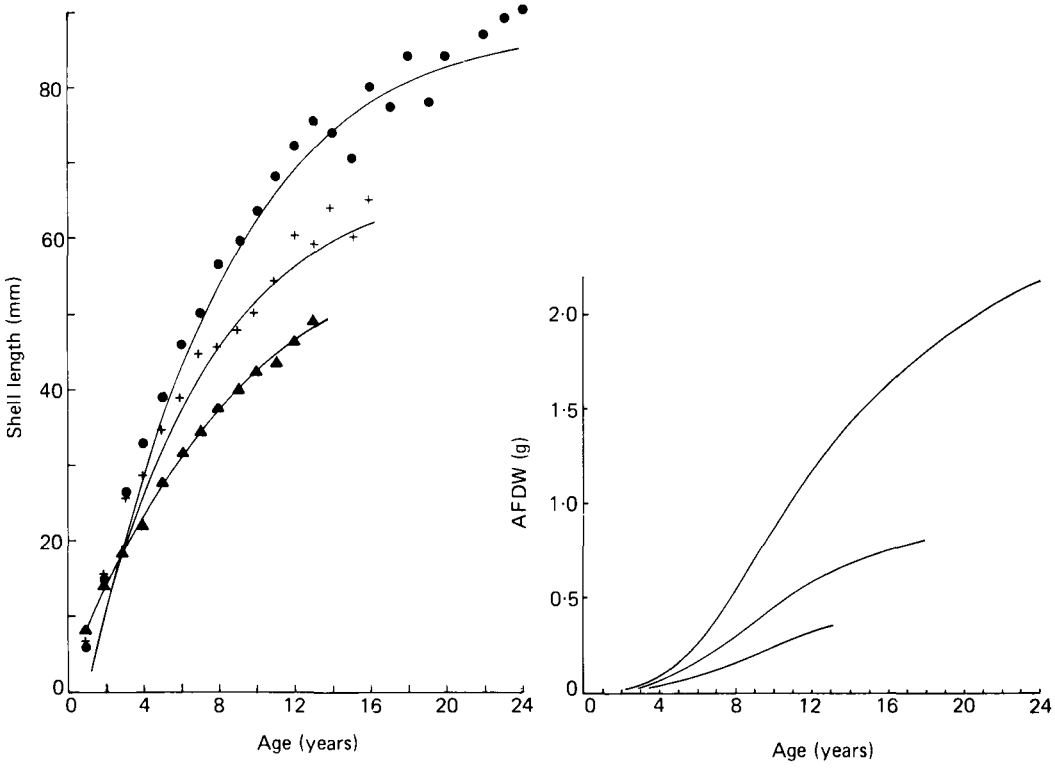

Fig. 8. *Mytilus edulis*: fitted von Bertalanffy growth models for shell at age. ▲, 33% aerial exposure; +, 13% aerial exposure; ●, 0% aerial exposure.

Fig. 9. *Mytilus edulis*: flesh weight growth trajectories predicted from von Bertalanffy models and June allometric equations relating shell length to ash-free dry weight (AFDW).

Gompertz model. Surface water temperature and D° data for Killary Harbour are given in Fig. 10 Total annual degrees were 4186 D°. The adjusted von Bertalanffy equations were as follows:

$$0\%\text{ aerial exposure: } l_D = 89[1 - e^{-0.33 \times 10^{-4}\,(D-5504)}]$$
$$13\%\text{ aerial exposure: } l_D = 69[1 - e^{-036 \times 10^{-4}\,(D-3988)}]$$
$$33\%\text{ aerial exposure: } l_D = 67[1 - e^{-0.23 \times 10^{-4}\,(D+1840)}].$$

Monthly modal shell lengths for cultured mussels from the first major settlements of the 1980 and 1981 seasons were taken from size frequency histograms. Modal AFDW was calculated for mussels from the 1980 settlement using the allometric equations given in Table 2. Growth trajectories for shell length and AFDW are given in Fig. 11. Shell growth is apparent from March/April until November. In suspended culture, a modal length of 43 mm was attained after approximately 18 months, whilst for comparison the fastest-growing mussles on the shore, at 0% aerial exposure, attain this length after about 6 years.

AFDW growth during the summer is sufficiently rapid in cultured mussels that

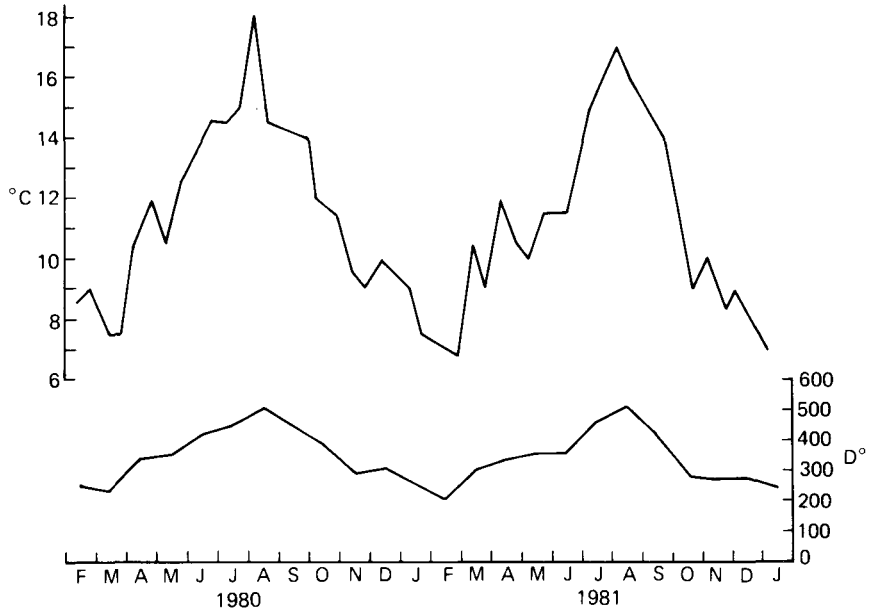

Fig. 10. Killary Harbour: annual cycle of sea-water temperature (°C) and day degrees (D°).

it is not possible to detect a fall in weight at the June/July spawning. However, the second spawning in August/September results in a marked descent on the AFDW growth trajectory, which is barely made up by the onset of winter.

DISCUSSION

Killary Harbour is characterized by low concentrations of PIM compared with other locations where bivalve food resources have been examined (Rodhouse, 1978; Widdows *et al.* 1979; Griffiths, 1980; Vahl, 1980). There is no apparent difference between PIM levels near the bottom at station A, in the vicinity of the wild mussel population, and in the water column at station D, where mussels are cultivated. Annual mean chlorophyll *a* concentrations are also similar at each station, which indicates that average phytoplankton density is similar throughout the Killary Harbour system over the period of primary production. POC concentrations are highest at the head of the fjord, where they do not correlate with chlorophyll *a* concentrations, indicating sporadic riverine input of allochthonous detrital carbon. Towards the mouth of the fjord POC concentrations are lower, and from April to October correlate with chlorophyll *a*, indicating that here the organic component of the seston is dominated by phytoplankton during the productive season. At these outer stations C:N ratio of the seston ranges from 6 to 8 from April to October, indicating a major contribution of phytoplankton carbon to the total POC. C:N ratios of seston at inner stations indicate fluctuation in the relative contribution of phytoplankton and detrital carbon to the total

seston. It is notable, however, that even at these inner stations seston C:N ratios usually remain low (< 12) over the year, so that a potential food resource is available when POC levels are sufficiently high.

Growth rate, in terms of shell length and AFDW, is considerably greater in cultivated mussels than in wild mussels. It takes approximately six years for the fastest growing wild mussels, at 0% aerial exposure, to attain a shell length and AFDW equal to that attained in one-and-a-half years in suspended culture. At higher levels on the shore, growth in wild mussels is further reduced due to the shorter time available for feeding (Seed, 1976).

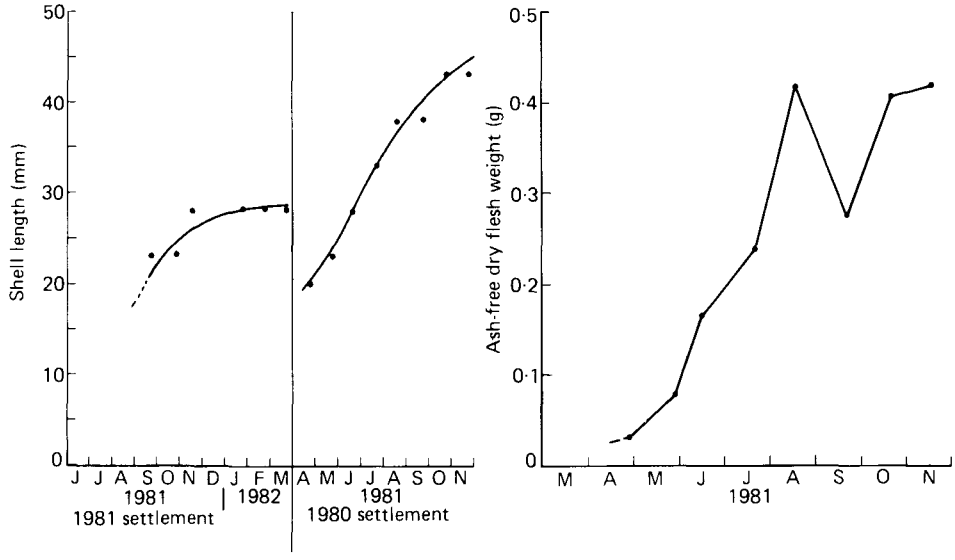

Fig. 11. *Mytilus edulis*. Shell length (A) and flesh weight (B) growth of cultured mussels.

The gametogenic and AFDW cycles of wild and cultured mussels are different. Cultured mussels spawn twice during the year, in May/June and August. Maximum AFDW is attained immediately prior to each spawning and drops sharply during spawning. After the second spawning AFDW continues to decline slowly through the autumn and winter and commences a rapid recovery in March/April. Wild mussels of all sizes spawn in the summer, in May/June, and there is a partial spawning by larger individuals in the early spring. The histological data suggest that this spawning was more intense in 1980 than 1981, but a peak of larval density in April 1981 and a settlement peak in May/June 1981 confirm that an early spawning occurred. Maximum AFDW is attained prior to the summer spawning and declines sharply during spawning. The gametes remain in the resting phase for the remainder of the summer, during which time AFDW increases. During September of both years there was a drastic loss in AFDW that was not associated with a spawning event. This was correlated with a period of sharply diminished salinity. From September until December larger mussels

(> 40 mm) increase in AFDW and there follows a protracted decline until March during which time the partial spawning occurs.

Small wild mussels, in common with cultured mussels, lose weight slowly through the autumn and winter and commence recovery in March. The gametogenic cycle of large wild mussels in Killary Harbour is similar to that described for populations in Normandy and western France (Lubet, 1957; Lubet & Le Gall, 1967; Le Gall, 1970). The gametogenic and AFDW cycle of cultivated mussels is similar to that described by Lutz *et al.* (1980) for cultured mussels in Maine, U.S.A.

We suggest that differences in the AFDW and gametogenic cycle between wild and cultivated mussels are due to differences in quantity and quality of the food resource close to the bottom and in suspended culture. Wild mussels inhabit an environment characterized by relatively high seston levels with a high energy content. Their available food consists of phytoplankton during the summer, mixed with variable amounts of detritus, which may itself vary in quality depending on age and origin (Tenore, 1977; Tenore & Hanson, 1980). From September until the following spring phytoplankton density is low but large mussels are able to utilize the food available, to increase AFDW until December, and spawn in early spring.

Cultured mussels inhabit an environment characterized by relatively low seston levels dominated in the summer by phytoplankton. Comparison with the data of Widdows *et al.* (1979) indicates that during the summer chlorophyll *a* concentrations in Killary Harbour exceed the maintenance ration for *M. edulis* ($= 130\ \mu g$ POC $.l^{-1} \approx 2{\cdot}4\ \mu g$ chlorophyll $a.l^{-1}$). This supports a high growth rate and enables cultured mussels to attain high AFDW during the summer and allows two summer spawning bouts, but after September there is steady weight loss as food levels decline in the water column. Incze, Lutz & Watling (1980) also suggest that phytoplankton is the major food source for mussels in suspended culture, and they report mortality associated with the onset of phytoplankton decline at the end of summer. Although growth rate may be enhanced in cultured mussels by the high quality of the food resource during the summer, this is probably also influenced by factors such as higher current speed near the surface replenishing food in the vicinity of rafts, and reduced disturbance by wave action and predators.

Bayne (1976) has classified the reproductive strategy of bivalves according to the relation between the spawning and storage cycle. Under this scheme *M. edulis* is a conservative species, utilizing storage products accumulated during the summer, for gametogenesis and vitellogenesis during the winter. This is followed by spawning in spring giving larvae the chance of exploiting the spring bloom characteristic of coastal waters in temperate latitudes. In opportunistic species gametogenesis occurs concurrently with the accumulation of energy reserves, resulting in a spawning in the summer, after the spring phytoplankton bloom. Wild *M. edulis* apparently exhibits both types of strategy in Killary Harbour, following the conservative strategy and spawning in early spring but then having

a second spawning which is opportunistic, being derived from resources accumulated during feeding concurrent with gametogenesis. Cultured mussels apparently have two opportunistic spawnings during the summer, the energy for which is derived from phytoplankton production which occurs concurrently with gametogenesis in the mussels.

We conclude that the physiological phenotype of *M. edulis* is a plastic character and is extremely susceptible to the influence of food quality and quantity. The food resource is highly variable spatially, over small distances in coastal ecosystems, and is dependent on primary production, the proximity of allochthonous carbon sources and distance above the sea bed, where particulates are concentrated. Spatially proximal populations may thus differ greatly in their cycles of gametogenesis and growth. Cultured mussels have a higher-amplitude seasonal cycle in AFDW than wild mussels, suggesting that they inhabit a superior environment during the summer which becomes stressful during the winter. It seems that the consequences, for a benthic species cultured in the pelagic realm, are that feeding conditions in the photic zone offshore are exceptional during periods of phytoplankton growth. However, during the autumn and winter months near-surface water becomes depleted of food and the mussels become stressed. Provided they are able to overwinter successfully, cultivated mussels are well situated for competing with zooplankton for the spring bloom resource. The shore and shallow sublittoral environment, for which mussels are adapted, is characterized by food consisting of a mix of living, moribund and dead phytoplankton cells and relatively higher levels of detritus, some of which is resuspended from the bottom. This food resource does not support maximal growth during the spring and summer, but contributes to maintenance and gametogenesis until the autumn and early winter, thus allowing the mussels to maintain a more stable energy balance throughout the year.

A comparison of the partitioning of carbon and nitrogen resources between soma, shell and gonad in wild and cultivated mussels will be dealt with in a later paper.

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