Aquaculture, 35 (1983) 151—161
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

ENERGY-FLOW IN A *MYTILUS EDULIS* CULTURE IN WESTERN SWEDEN

RUTGER ROSENBERG[1] and LARS-OVE LOO[2]

[1] *Institute of Marine Research, Box 5, 453 00 Lysekil (Sweden)*
[2] *Tjärnö Marine Biological Laboratory, Pl. 2781, 452 00 Strömstad (Sweden)*

(Accepted 4 January 1983)

ABSTRACT

Rosenberg, R. and Loo, L.O., 1983. Energy-flow in a *Mytilus edulis* culture in western Sweden. *Aquaculture*, 35: 151—161.

Energy-flow is described for a blue mussel long-line culture of 4 500 m^2 which settled in June 1978 and was harvested in March 1980. Food quality varied with season. Phytoplankton blooms contained >95% of the seston protein and carbohydrate. However, in winter, >90% of these substances were bound in detritus. Consequently mussel energy content declined in both winters. Current speed had a theoretical linear relationship with long-line numbers during non-winter months. Particulate retention in the culture centre was 15—50%, suggesting culture numbers could be nearly doubled without significant growth depression.

Estimates of biomass, production, respiration, assimilation, ingestion and faeces production were incorporated into an energy-flow diagram for the 571-day study. The highest assimilation, 751 kJ m^{-2} day^{-1}, took place in the second autumn. Overall respiration was 58%, production was 42% of assimilation, and 64% production remained as the mussel terminal biomass. Epifauna biomass was about 1% of the mussel biomass after 15 months. Production/mean biomass for the complete study was 2.7 and the yield at the best time for harvest (November—December 1979) was close to 36 000 g wet weight per m^2. An 80% assimilation efficiency estimate gave a faeces production close to that measured as the sedimentation rate and was considered a better evaluation than a 60% assimilation efficiency.

INTRODUCTION

Blue mussel cultivation is rapidly increasing in the Skagerrak archipelago of north western Sweden. The spat are caught and grown on 50 mm × 6 m polypropylene straps attached to 180-m long-lines. After 1.5 years, the mean length of non-thinned out mussels grown at the 0—2 m depth was 60 mm (Loo and Rosenberg, 1983). This is broadly similar to the results of Lutz et al. (1980) in Maine, U.S.A., and most other European culture studies except for Spain (Tenore and Gonzales, 1976) where the average yearly rate given (> 70 mm) only applied to the large mussels left after thinning out.

The development of the blue mussel culture community has been des-

0044-8486/83/$03.00

cribed by Loo and Rosenberg (1983) and results from other studies of the same culture are given elsewhere (Dahlbäck and Gunnarsson, 1981; Hagström and Larsson, 1982; Romare et al., 1982; Wiigh-Mäsak, 1982; Larsson, 1983; Lännergren, in MS; Mattsson and Lindén, 1983).

MATERIAL AND METHODS

The energy content of *Mytilus* calculated from 1 mg flesh dry weight (DW) was equal to 20.51 J (Dare and Edwards, 1975), and from 1 mg ash-free dry weight (AFDW) of the shell was equal to 21.10 J as described for *Scrobicularia plana* (da Costa) (Hughes, 1970). The energy content of the shells of these two species was considered to be similar. According to our measurements, dry weight (inclusive of shell) multiplied by 2.6 gave the total live weight.

Respiration was calculated from $Y = 0.320 \cdot X^{0.700}$ (Krüger, 1960; the experiment was conducted in August at 15°C), during the periods 780814 — 781108 and 790708 — 791130 (the dates are given as year, month and day), where Y = ml O_2 h^{-1} and X = g flesh dry weight. From 781108 — 790411 and 791130 — 800307, respiration was calculated as $Y = 0.525 \cdot X^{0.930}$ (Krüger, 1960; an experiment in March also at 15°C) but was reduced by a factor of 1.6 as results were obtained in experiments at the Tjärnö Laboratory in temperatures between -1.0 and +4.8°C (Loo, in MS). One ml O_2 corresponds to 19.88 J (Riisgard and Randlöv, 1981).

For primary production, the following equivalents were used: 1 mg C = 13.30 cal = 55.67 J (Vollenweider, 1965). The energy content in material deposited by the culture was estimated from the formula:

1 mg DW = 0.632 + (0.086 × % organic carbon) cal

(Parsons et al., 1979). Equations used were:

$A = P+R$, $I = A/A_e$ and $F = I-A$

where A is assimilation, P is production, B is biomass, R is respiration, I is ingestion, A_e is assimilation efficiency and F is faeces production. Data on the mussels production (P) and biomass (B) are taken from Loo and Rosenberg (1983), and on seston biomass (S_B) and seston production (S_P) from Lännergren (in MS).

RESULTS AND DISCUSSION

Settlement of *Mytilus edulis* was recorded in June 1978 (Romare et al., 1982) and the development of the culture was followed from 14 August 1978 to 7 March 1980. The mussel culture was the same as described in more detail by Loo and Rosenberg (1983). In that paper the development of the mussel culture through different time phases is described. To facilitate comparisons, the various energy units have been calculated for each of these time intervals (Table I), as well as per m^2 (the total area was 4 500 m^2).

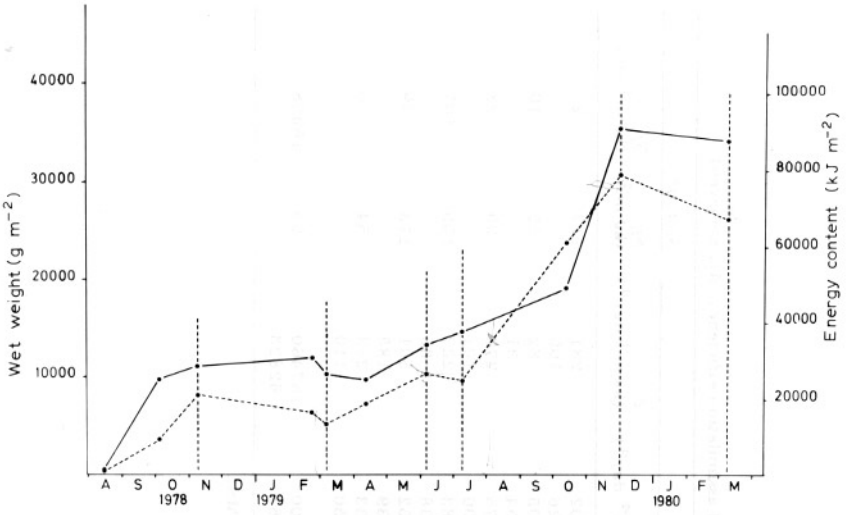

Fig. 1. The development of *Mytilus edulis* in a cultivation at Tjärnö shown as energy content in kJ m^{-2} (broken line) and as g wet weight m^{-2} including shells (solid line). The vertical broken lines indicate the seasons (autumn, winter etc) to which reference is made in Table I and in the text.

Quantities per m^2 are, however, dependent on spacing of the bands and the distance between the long-lines. The biomass accumulated over the whole period of 571 days, both in kJ and live weight, is presented in Fig. 1. The energy content of the shell was 22% of the total energy content of the mussel. The highest biomass-increments (production) were noted in the autumns of 1978 and 1979. Both these periods coincided with high levels of phytoplankton (Table I). Phytoplankton levels were also high during the summer of 1979 but at this time a drop in biomass was recorded as a result of prior gonad release.

Phytoplankton and bacterioplankton

Primary production outside the mussel culture was estimated at 222 g C m^{-2} $year^{-1}$ in 1979 (Lännergren, in MS). In the size fraction of <200 μm, about half of the production was by plankton of <5 μm over the year. During summer, these small plankton constituted about 70% of the total energy content. Lännergren (in MS) also noted significant seasonal variations in the quality of seston. During blooms, more than 95% of the protein and carbohydrate in the seston was bound in phytoplankton while, for a 3-month period in winter (1979—1980), 90% was bound in detritus. Energy content in seston, taken as an average over the 1—5 m depth, was 6 kJ m^{-3} in winter and reached a peak of 45 kJ during autumn blooms. For energy-flow measurements, the energy in the water is of importance and not the values of primary production per se. However, during experiments, excretion from the mussels was shown to stimulate primary production (Lännergren, in MS).

TABLE I

Energy values (kJ) at different time periods (year, month, day) during the study. (two options of assimilation efficiency, A_e, are given)

Period (days)	Mussels*							Seston*	
	B (kJ m^{-2})	P (kJ m^{-2} day^{-1})	R (kJ m^{-2} day^{-1})	A (kJ m^{-2} day^{-1})	A_e(%)	I (kJ m^{-2} day^{-1})	F (kJ m^{-2} day^{-1})	S_B (kJ m^{-2})	S_P (kJ m^{-2} day^{-1})
Autumn, 86 days	21153	273	148	421	60	702	281	117	27
(780814—781108)					80	526	105		
Winter, 118 days	13342	-5	128	123	60	205	82	55	10
(781108—790306)					80	154	31		
Spring, 91 days	26750	226	179	405	60	675	270	99	28
(790306—790605)					80	506	101		
Summer, 33 days	24326	96	254	350	60	583	233	135	107
(790605—790708)					80	438	88		
Autumn, 145 days	79050	400	351	751	60	1252	501	113	39
(790708—791130)					80	939	188		
Winter, 98 days	67295	4	436	440	60	733	293	54	10
(791130—800307)					80	550	110		
Whole period,	67295	105014	146126	251140	60	418600	167460	99	16358
571 days (kJ m^{-2})					80	313963	62823		

* Data of B and P based on Loo and Rosenberg (1983), and S_B and S_P based on Lännergren (in MS).

An increased production could not, however, be recorded during a 24-h study of the culture, and the production of bacterioplankton was found to be similar at a reference station: $7—10^8$ bacteria l^{-1} day^{-1}, approximately corresponding to 0.1 mg wet weight l^{-1} (Hagström and Larsson, 1982). Thus, despite the fact that the weak tidal flow only transported the water 400 m backwards and forwards during each cycle (Larsson, 1983), it is not likely that released nutrients stimulated primary production in the vicinity of the culture to any greater extent.

Food as a limiting factor

The decrease in energy content of the blue mussels during winter was apparently due to low seston concentration and poor food quality. Plant detritus is a poor food source for mussels (Williams, 1981). Incze and Lutz (1980) in Maine, U.S.A., noted seasonal variations in seston quality and suggested this may significantly affect mussel growth. Wallace (1980) also demonstrated that food was the limiting factor for growth during winter in northern Norway. Thus, quantity and quality of food were limiting factors for mussel growth during the winter at Tjärnö.

Energy-flow

The respiration values are brief estimates taken from the literature. Respiration per m^2 generally increased with culture age (Table I). Assimilation is dependent on food availability and increases with mussel size. The highest assimilation rate (estimated to be 751 kJ m^{-2} day^{-1}) occurred during the second autumn and coincided with a bloom of dinoflagellates (Lännergren, in MS). The assimilation efficiency (A_e) may vary with season, temperature, food concentration and quality, and mussel size. From 8 May — 15 August, A_e was measured in the laboratory using mussels from the culture supplied with natural surface sea water, 27 recordings gave a mean A_e of 72% (range 44—92%, S.D.=16). During the 1981 spring bloom, 5 recordings at temperatures ranging from -1.0 to +4.8°C gave a mean of 67% (range 53—81%, S.D.=11) (Loo, in MS). Therefore, we picked two options for A_e in Table I: 60 and 80%. The lower percentage resulted in the higher ingestion rate needed. The highest ingestion (1252 kJ m^{-2} day^{-1}) was calculated in this way during the second autumn. Faeces production estimates were also highest during this period.

The Table I data for 571 days are presented diagrammatically in Fig. 2. In the diagram $A = P+R$, and the estimates show that respiration provided 58% and production 42% of assimilation. Of the estimated total production, 64% was retained in the culture as mussel biomass. Thus about 36% in weight of the production was lost during the culture period due to gamete production, predation, natural mortality and mussels falling to the bottom. The eliminated biomass (including shells) was estimated to be 38 456 kJ m^{-2}

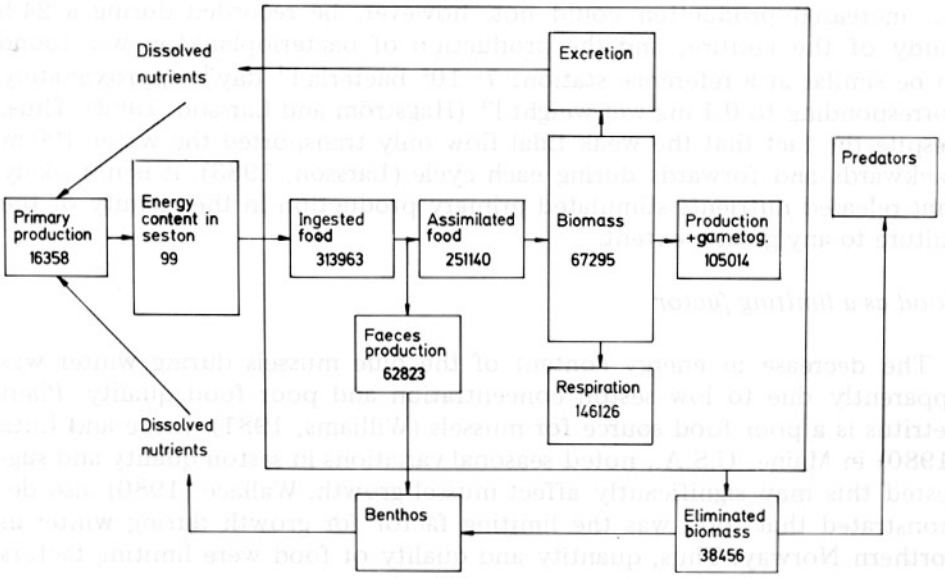

Fig. 2. Simplified energy flow diagram in kJ m^{-2} of *Mytilus edulis* (including shells) based on values for the whole mussel culture period of 571 days with an assimilation efficiency of 80% (see Table I).

(Loo and Rosenberg, 1983), a figure which corresponds well with that predicted by the energy-flow diagram, where P-B= 37 719 kJ m^{-2}. This method of calculating production probably gave a slight underestimate as suggested by Loo and Rosenberg (1983). The first period subsequent to settling was, however, not covered in this study and results from this would probably have given a somewhat higher production. Excretion by the mussels (dissolved organic material, such as amino acids, or inorganic nutrients) was not measured but is indicated in the diagram.

Two $P/\bar{B}$ ratios have been calculated, both based on a mean biomass ($\bar{B}$) calculated from the figures given in Table I. The annual $P/\bar{B}$ from 780814 — 790708 was calculated as 2.2. and the $P/\bar{B}$ for the whole period was 2.7. The validity of these ratios will not be discussed here but they seem low for as productive a system as a mussel culture. It has, however, been shown above that a large part of production was stored as mussel biomass. Over the entire period, elimination was calculated to be 37% of the production over the 0—6 m depth (Loo and Rosenberg, 1983). The high biomass of the mussels will create low $P/\bar{B}$ ratios but this should, however, be compared to the highest yield which was approximately 36 000 g m^{-2} live weight (Fig. 1).

Based on the assimilation figure, the energy demand as ingested food was calculated for an assimilation efficiency of both 60 and 80%. The higher efficiency of 80% was used in Fig. 2 and this resulted in a total ingestion requirement of 313 963 kJ m^{-2} of which 62 823 kJ m^{-2} (20%) was released as faeces. Estimates of sedimentation from mussel cultivation made over a

period of four months were recently presented by Dahlbäck (personal communication, 1982) in an extension of the study by Dahlbäck and Gunnarsson (1981). The average sedimentation rate was 2.1 g C m^{-2} day^{-1} which, with an average carbon content in the sediments of 19%, corresponds to an average energy content for the whole study period of 64 834 kJ m^{-2}. This agrees well with the calculated faeces production of 62 823 kJ m^{-2}. A somewhat lower rate of sedimentation than faeces production would, however, be expected as some of the faeces will settle outside the culture. Thus, an assimilation efficiency of approximately 80% would appear to be the best estimate. Cabanas et al. (1979) reported an assimilation efficiency of 79% from a raft-culture in Ria de Arosa, Spain, and Winter (1977) lists assimilation efficiencies of 69—84%.

The energy content in the seston is given in Fig. 2 as a mean standing stock for the whole period and the total primary production is summed over 571 days (from Lännergren, in MS). These values do not, when used alone, add much to the energy-flow diagram but in combination with different current speeds they could be useful in determining the capacity of the area for mussel culture. The ratio between primary production and secondary production of *Mytilus* for the whole period was 0.2, which indicates the importance of currents in transporting food to the mussels.

Epifauna and benthos

The high annual sediment accumulation of approximately 10 cm detritus under the culture gradually devastated the benthic infauna. The opportunistic polychaetes, *Capitella capitata* and *Scolelepis fuliginosa*, were favoured by the organic load and, in April 1980, were recorded in numbers close to 40 000 individuals (ind.) per m^2 (Mattsson and Lindén, 1983). We have noted that part of the bottom was periodically covered by the white sulphur bacteria, *Beggiatoa*, and anaerobic mineralization of detritus is important below the sediment surface. Fish (e.g. cod, eel and flat fish) periodically gathered in the culture, sometimes in great numbers, and ate fallen mussels. After about one year, 2 800 mussels with a live weight of 9 400 g m^{-2} were recorded under the long-lines (Mattsson and Lindén, 1983).

In the mussel culture in Sweden, the epifauna associated with the mussels made up about 1% of the weight after 15 months and played a negligible role compared with the mussels in transfer of energy in the community. In the Rias de Arosa, Spain, however, a strong epifaunal community developed among the mussels with an approximate production of 10% of that of the mussels (Tenore et al., 1982). Ancillary production of biota and detritus that serves as food for a detritus-based food chain was estimated as being 67% of the mussel production on the rafts in Spain. Much of the detritus produced by the mussels was utilized by the raft epifauna before it reached the bottom. Benthic fauna under the rafts was stressed by sediment instability and low oxygen on the bottom and a pioneering community dominated

by the polychaete, *Spiochaetopterus costarum*, was established. Thus, bottom and benthic fauna changed in a way similar to that at Tjärnö.

It seems unlikely that the Swedish mussel culture absorbs such large quantities of seston as to impoverish other hard-bottom epibenthic animals in its vicinity. The effects on the soft-bottoms may be considered to be of temporal nature, i.e. if culture ceased, a recovery of the benthic community would occur in a matter of 3—8 years as shown in a former organically polluted area south of Tjärnö (Rosenberg, 1976).

Limiting factors for mussel culture

Assuming unlimited available space, the two main interrelated ecological factors limiting the size of mussel cultures are seston concentration (food ration) and current speed. Two examples are given in Fig. 3 to illustrate the importance of these factors. The calculations are based on Incze and Lutz (1980). A one-year-old culture of the long-line type was used, similar in size to the Tjärnö culture; it was oriented perpendicularly to the current. At that time, the mean dry weight of a mussel without shell was 0.28 g. A maximum filtration rate of 3.2 l h^{-1} ind.$^{-1}$ was used in the calculations (Möhlen-

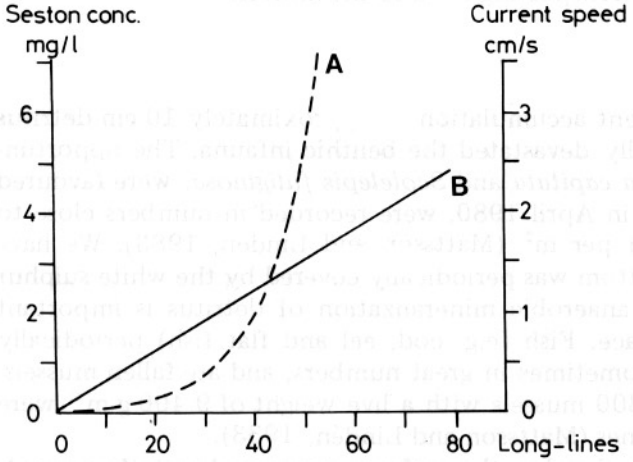

Fig. 3. Seston concentration in mg l^{-1} (A) and current speed (B) in relation to the number of long-lines. Data used for the diagrams:

	A	B
Length of long-line (m)	180	180
Depth (m)	6	6
Current speed (cm s^{-1})	1	*Y*
Distance between band (m)	0.5	0.5
Mussels (ind. m^{-1})	518	518
Filtration rate (3.2 l h^{-1} ind.$^{-1}$)	3.2	3.2
Seston before passage (mg l^{-1})	*Y*	1.1
Seston after passage (mg l^{-1})	0.05	0.05
Number of long-lines	*X*	*X*

berg and Riisgard, 1979). The seston concentration was measured at Tjärnö in front of the culture, whereas a figure of 0.05 mg l^{-1} (equal to maintenance-concentration — Riisgard and Randlöv, 1981) was chosen at the lee of the culture. The number of blue mussels was set at 518 ind. m^{-1}, which represent a normal density in the culture after about one year.

In the first example (A) with a current speed of 1 cm s^{-1}, the seston concentration needed to support an increasing number of long-lines increased exponentially. However, at this low current speed, seston concentrations up to 1 mg l^{-1} could theoretically provide adequate nutrition for more than 30 long-lines. In this example, the quality of the food and food competitors in the *Mytilus* community have been disregarded.

In example B the seston concentration was taken to be constant at 1.1 mg l^{-1}. The current speed requirement increased linearly with an increasing number of long-lines. Mussels on about 30 long-lines should be able to maintain their metabolism in a current speed of 1 cm s^{-1}. It should be noted that both higher seston concentrations and increased current speeds are needed for growth. In conclusion, the results show that any increase in the number of long-lines is dependent on a corresponding increase in current speed and on a considerable increase in the quantity of food. Current speed (water exchange) was found to be a vital factor in high-density mussel cultures.

Let us assume that the mussel culture investigated at Tjärnö with its fourteen 180-m long-lines and a breadth of 25 m was oriented perpendicularly to the current and that the seston was filtered with equal efficiency by each mussel. We know the mean energy content of seston during different periods (Table I). With an assumed assimilation efficiency of 80%, and using the formula:

$$\text{current speed} = 25\ \text{m} \cdot I/S_B$$

where 25 m is the breadth of the culture, it is possible to calculate the current speed in which mussels would have theoretically depleted the seston. Calculated current speeds were 0.1 cm s^{-1} during the summer of 1979 and 0.2 cm s^{-1} during the following autumn. Thus, at the time, food was not a limiting factor for growth. The same seston concentration (Table I) could also be used to calculate reductions of seston at different current speeds. The reductions of seston during the autumn of 1979, from a mean energy content of 113 kJ m^{-2} (18.8 J l^{-1}), were 21, 11 and 5% in the current speeds 1, 2 and 4 cm s^{-1} respectively.

Bearing in mind the difference between theoretical and 'in situ' results and assuming an even supply of the available seston throughout the culture, a final calculation can be made to determine the number of long-lines capable of being supported by a given seston maintenance concentration for the mussels (1 J l^{-1} equal to 0.05 mg l^{-1} according to Riisgard and Randlöv, 1981). In the autumn of 1979, assuming an assimilation efficiency of 80%, the number of long-lines theoretically capable of support should be 55, 110 and 221 at current speeds of 1, 2 and 4 cm s^{-1} respectively. The numbers

seem excessive and with such a high density of mussels it is likely that the specimens at the centre and those in the lee of the current would more or less starve. However, the figures imply that the 14 long-lines used during this investigation could be increased without detriment to the rate of growth.

Measurements in the culture area at Tjärnö suggest, however, that the above calculations are too optimistic as to the number of long-lines that could be laid out. Lännergren (in MS) recorded a mean reduction in particulate content at the centre of the culture of 30—50% of the fraction <200 μm, and 15—40% of the fraction <5 μm (based on 19 measurements in 1979 and 12 in 1980). Another measurement, where water was filtered on a 1.2 μm GF/C filter, gave a mean reduction of about 40% in the centre of a mussel culture. One explanation for the difference between these values and the theoretical calculations is that growing mussels consume more seston than is strictly needed to maintain metabolism and that other members of the mussel community will take particles from the water. In Rias de Arosa, Spain, mussels in a raft-culture retained 30% of the available carbon, 42% of the available nitrogen and 60% of the available chlorophyll a at a current speed of 5 cm s^{-1} (Cabanas et al., 1979).

According to the field experiments, the amount of food available in the same restricted body of water was sufficient to support approximately double the number of long-lines used in Sweden. If the culture was to be extended beyond these limits, then new locations with independent food supplies should be established.

ACKNOWLEDGEMENT

We gratefully acknowledge the support provided by The Bank of Sweden Tercentenary Foundation, and thank Dr. N. Kautsky, Dr. P. Rodhouse and Mr. C. Wheatley for valuable comments on the manuscript.

REFERENCES

Cabanas, J.M., Gonzalez, J.J., Mariño, J., Perez, A. and Roman, G., 1979. Estudio del mejellon y de su epifauna en los cultivos flotantes de la Ria de Arosa. III. Observaciones previas sobre la retencion de particulos y la biodeposicion de una batea. Bol. Inst. Esp. Oceanogr., 5 (268): 45—50.

Dahlbäck, B. and Gunnarsson., L.A.H., 1981. Sedimentation and sulfate reduction under a mussel culture. Mar. Biol., 63: 269—275.

Dare, P.J. and Edwards, D.B., 1975. Seasonal changes in flesh weight and biochemical composition of mussels (*Mytilus edulis* L.) in the Conwy Estuary, North Wales. J. Exp. Mar. Biol. Ecol., 18: 89—97.

Hagström, A. and Larsson, A.M., 1982. Pelagic bacteria and mussel culture. (In Swedish with English summary.) Meddelande Havsfiskelaboratoriet, Lysekil 286, 21 pp.

Hughes, R.N., 1970. An energy budget for a tidal-flat population of the bivalve *Scrobicularia plana* (da Costa). J. Anim. Ecol., 39: 357—381.

Incze, L.S. and Lutz, R.A., 1980. Mussel culture: an east coast perspective. In: R.A. Lutz (Editor), Mussel Culture and Harvest: a North American Perspective. Elsevier Scientific Publishing Company, Amsterdam, pp. 99—140.

Krüger, F., 1960. Zur Frage der Grössenabhängigkeit des Sauerstoffverbrauchs von *Mytilus edulis* L. Helgoländer wissenschaftliche Meeresuntersuchungen, 7: 125—148.

Larsson, A.M., 1983. Hydrographical and chemical observations in a coastal area with mussel farming, western Sweden. Meddelande Havsfiskelaboratoriet, Lysekil 291 (in press).

Loo, L.O. and Rosenberg, R., 1983. *Mytilus edulis* culture: growth and production in western Sweden. Aquaculture, 35: 137—150.

Lutz, R.A., Incze, L.S. and Hess, C.T., 1980. Mussel culture in heated effluents: biological and radiological implications. In: R.A. Lutz (Editor), Mussel Culture and Harvest: a North American Perspective. Elsevier Scientific Publishing Company, Amsterdam, pp. 166—192.

Mattsson, J. and Lindén, O., 1983. Benthic macrofauna succession under mussels, *Mytilus edulis* L. (Bivalvia), cultured on hanging long-lines. Sarsia, 68 (in press).

Möhlenberg, F. and Riisgard, H.U., 1979. Filtration rate, using a new technique, in thirteen species of suspension-feeding bivalves. Mar. Biol., 54: 143—148.

Parsons, T.R., Takahashi, M. and Hargrave, B., 1979. Biological Oceanographic Processes, 2nd edition. Pergamon Press, Oxford, 332 pp.

Riisgard, H.U. and Randlöv, A., 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar. Biol., 61: 227—234.

Romare, P., Hakansson, M. and Rosenberg, R., 1982. Settlement and subsequent dispersion of the blue mussel *Mytilus edulis* L. on the Swedish west coast. Meddelande Havsfiskelaboratoriet, Lysekil 285, 16 pp.

Rosenberg, R., 1976. Benthic faunal dynamics during succession following pollution abatement in a Swedish estuary. Oikos, 27: 414—427.

Tenore, K.R. and Gonzalez, N., 1976. Food chain patterns in the Ria de Arosa, Spain: an area of intense mussel aquaculture. In: G. Persoone and E. Jaspers (Editors), 10th European Symposium on Marine Biology, Ostend, Belgium, Vol. 2. Universa Press, Wettern, Belgium, pp. 601—619.

Tenore, K.R., Boyer, L.F., Cal, R.M., Corral, J., Garcia-Fernandez, C., Gonzalez, N., Gonzalez-Gurriaran, E., Hanson, R.B., Iglesias, J., Krom, M., Lopez-Jamar, E., McClain, J., Pamatmat, M.M., Perez, A., Rhoads, D.C., de Santiago, G., Tietjen, J., Westrich, J. and Windom, H.L., 1982. Coastal upwelling in the Rias Bajas, NW Spain: Contrasting the benthic regimes of the Rias de Arosa and de Muros. J. Mar. Res., 40: 701—772.

Vollenweider, R.A., 1965. Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. Mem. Ist. Ital. Idrobiol. Suppl., 18: 425—457.

Wallace, J.C., 1980. Growth rates of different populations of the edible mussel, *Mytilus edulis*, in north Norway. Aquaculture, 19: 303—311.

Wiigh-Mäsak, P., 1982. Season-dependent dynamics in mussel cultures in Mollösund and Lyrösund, Bohuslän, Sweden. (In Swedish with English summary). Meddelande Havsfiskelaboratoriet, Lysekil 284, 24 pp.

Williams, P., 1981. Detritus utilization by *Mytilus edulis*. Estuarine, Coastal and Shelf Sci., 12: 739—746.

Winter, J.E., 1977. Suspension-feeding in lamellibranchiate bivalves, with particular reference to aquaculture. Medio Ambiente, 3: 48—69.