OPHELIA 35 (2): 123-131 (May 1992)

FILTRATION, ASSIMILATION, RESPIRATION AND GROWTH OF *MYTILUS EDULIS* L. AT LOW TEMPERATURES

Lars-Ove Loo
University of Göteborg Marine Research Station at Kristineberg,
S-450 34 Fiskebäckskil, Sweden

ABSTRACT

Studies of absorption, respiration and growth of *Mytilus edulis* L. were conducted at low temperatures, -1 to +4.8°C, with a natural seston composition. The bivalves actively ingested seston at -1°C and showed an absorption efficiency between 53 and 81% during the experimental period. The respiration rates ranged between 0.12 and 0.28 ml O_2 h^{-1}ind.$^{-1}$ and the specific growth rate was 0.7% shell free dry weight per day. The results suggest that *M. edulis* can utilize the phytoplankton spring-bloom in boreal waters even at low temperatures.

INTRODUCTION

In boreal waters the spring-bloom of phytoplankton is the starting point for secondary production each year. In some temperate and boreal areas the spring primary production period can be short, a few weeks only, but the resulting biomass can be extensive. Zooplankton abundance in some areas is low at this time (Bathmann et al. 1990) but part of the phytoplankton biomass may be consumed by benthic suspension feeders (Rosenberg & Loo 1983). In Scandinavian waters, such as the Skagerrak and Kattegat, the temperature during the spring-bloom is usually 0°C. It is known that suspension-feeding bivalves, e.g. *Cerastoderma edule* (Loo & Rosenberg 1989) and *Ostrea edulis* (E. M. Rödström, Tjärnö Marine Biological Laboratory, pers. com.) cannot feed at such low temperatures, but growth and function in the bivalve *M. edulis* have only previously been studied at temperatures above 2°C (Jørgenen et al. 1990) and earlier by Kautsky (1982) and Kautsky & Wallentinus (1980) from the Baltic.

The purpose of this study is to investigate whether the blue mussel *M. edulis* is capable of feeding and absorbing food at temperatures around 0°C. *Mytilus edulis* is a quantitatively dominating species on hard substratum in shallow waters of the north Atlantic and extensive aquaculture renders it commercially important in many countries.

I acknowledge the constructive review and comments by Dr. P. Jonson, Prof. N. Kautsky, Prof. R. Rosenberg, Dr. I. Svane, an anonymous reviewer and Mr. C. Wheatley. The study was financed by the Bank of Sweden Tercentenary Foundation.

MATERIAL AND METHODS

The experiments were performed during the period 29 January to 5 April 1981 at Tjärnö Marine Biological Laboratory. Surface sea water at a salinity of 20-30‰, with a natural particle composition was pumped directly into the laboratory from a depth of 1.5 m.

The ingestion rate was determined as follows: At the beginning of the experiments sixteen bivalves with a mean length of 40.3±0.5 (x±SD) mm were chosen. Ten of these were dried and the mean SFDW (shell free dry weight) per ind. was determined at the start of the experiment. Each of the remaining six bivalves was placed inside individual Plexiglass tubes, length 80 mm and diameter 30 mm, fitting the size of the mussels. SFDW was determined in April after the experiment.

The ingestion rate was calculated as follows: I = (Sb-Sa) F, I = ingestion rate (mg AFDW h^{-1}), Sb = seston concentration in the inflow water, Sa = seston concentration after passage, and F = water-flow through the Plexiglass tube. The flow was not exactly the same for each of the 6 bivalves at each experimental period.

The seston concentration in the water flow was determined by examining 2 l of water before and 2 l after passage through the tubes. The water was subsequently filtered through glass microfibre filters, Whatman GF/C, with a pore size of 1-2 μm. *Mytilus edulis* particle-capture retention-efficiency is about 100% at a particle size down to 1-2 μm and below this, retention efficiency declines significantly (Vahl 1972). Before filtration, the filters were washed with distilled water, heated to 500°C, and weighed. The filters together with the filtrate were then washed with distilled water, dried at 70°C and weighed. The filters were heated to 500°C and weighed again. DW (dry weight) and AFDW (ash free dry weight) of the filtrates were thus determined.

In order to determine the confidence limits of the filtrate measurements (DW) a regression line between a mean value and a 95-% significance level was calculated: ($Y = 0.005 + x\ 9.3\ 10^{-3}$) Y = confidence interval at a 95% significance level, x = filtrate in mg. A Mettler ME 30 balance was used to determine weight.

To estimate absorption efficiency, faeces in the Plexiglass tubes were collected by filtering through GF/C filters. After 20 h of exposure DW and AFDW were determined. Calculation of absorption efficiency was carried out according to Conover (1966).

Respiration at different flow velocities was recorded by measuring the oxygen concentration in the inflow and again in the outflow water after passing one experimental tube containing 16 mussels. An oxygen probe, YSI Model 57, connected to a recorder was used. The oxygen content in the water before and after

Table 1. Temperature, salinity, seston concentration, absorption efficiency and respiration of the blue mussel *Mytilus edulis* L. during the spring-bloom 1981 at Tjärnö Marine Biological Laboratory.

Date	29 Jan	19 Feb	3 Mar	9 Mar	5 Apr
Temperature (°C)	1.5	-1	-0.5	0	4.8
Salinity (‰)	25.8	27.0	20.9	19.5	19.2
Seston concentration					
DW (x±SD) (mg l^{-1})	0.93±0.12	3.03±0.27	2.94±0.20	2.29±0.18	0.67±0.08
AFDW (x±SD) (mg l^{-1})	0.43±0.06	0.76±0.07	1.80±0.08	1.47±0.07	0.39±0.02
Absorption efficiency					
(x±SD) (%)	53±3	74±2	59±3	69±3	81±4
Number of individuals	6	2	6	6	6
Respiration					
(x±SD) (ml h^{-1} $ind.^{-1}$)	0.12±0.01	0.14±0.01	0.18±0.01	0.16±0.02	0.28±0.04
Number of measurements	4	4	4	4	4
Number of individuals	16	16	16	16	16

the mussels was measured by alternatively switching the flowing water to the probe. Four measurements were done at each experimental time (Table 1).

RESULTS

Five experiments were performed during the spring-bloom period at temperatures between -1 and 4.8°C and the results are presented in Table 1. Temperature and salinity in the laboratory sea water during the course of the experiment are shown in Fig. 1, and corresponded to natural conditions in the bay outside the laboratory.

Variation in the seston concentrations in laboratory sea water reflects natural development of the spring-bloom. Seston concentrations are shown both as DW and AFDW in Fig. 2. AFDW of the seston content had a smaller variation than DW. The dominant phytoplankton species during the spring-bloom were *Ceratium tripos, Skeletonema costatum* and *Chaetoceros socialis*.

The ingestion rate of *M. edulis* as a function of water flow is shown (Fig. 3). This figure shows that *M. edulis* actively ingest food particles at temperatures down to -1°C (Table 1). At two dates, 29 January and 9 March ingestion rate increased with increased flow.

Absorption efficiencies from the 6 bivalves are given in Table 1. The absorption efficiency varied between 81 and 53% with the highest value at 4.8°C and the lowest at 1.5°C. But the second-highest value was observed at temperature of -1°C.

Respiration varied between 0.12 and 0.28 ml O_2 h^{-1} $ind.^{-1}$. Lowest respiration was found at the beginning of the period and highest at the end (Table 1). The mean length of these mussels was at the beginning of the experiments 40.4±0.5 (x±SD) mm.

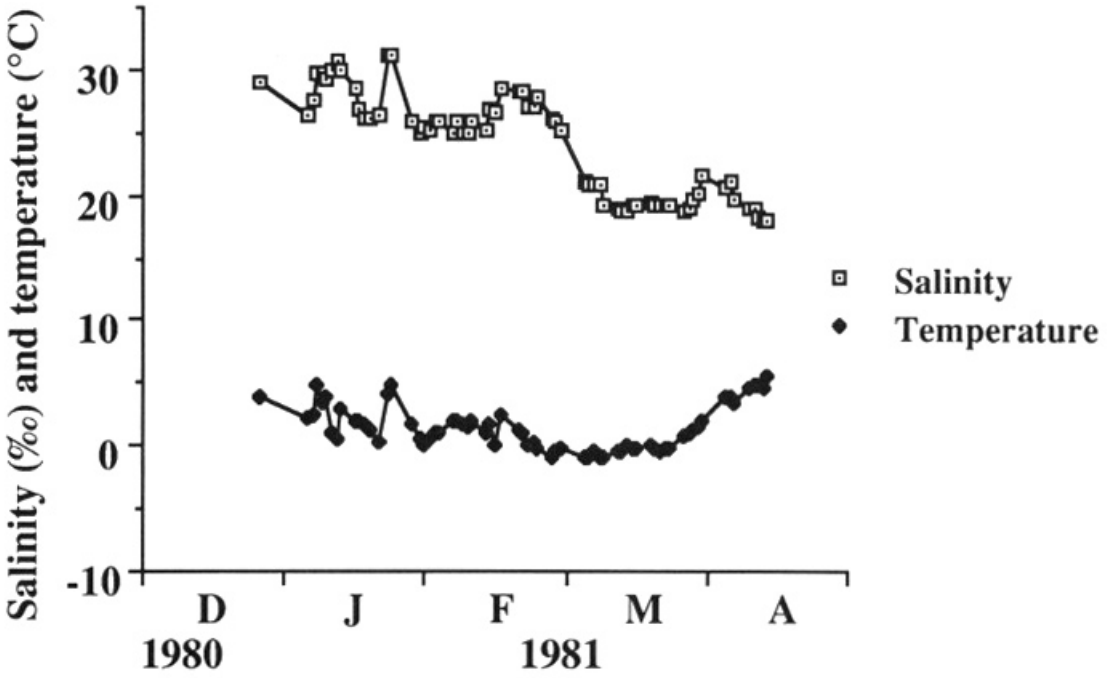

Fig. 1. Salinity and temperature in the experimental sea water during the study period.

The average individual weight of the mussels at the start of the experiments was 0.392±0.042 SFDW (g) and 65 days later was found to be 0.602±0.106 SFDW (g). Consequently, growth was 0.210 SFDW (g) during 65 days at a specific growth rate of 0.7% per day (=ln(0.602)-ln(0.392)) 100(65). The mean flow rate through the tubes between experiments was about 15 l h^{-1}.

DISCUSSION

Ingestion rate

Ingestion rates of bivalves at relatively low temperatures have been reported for some species (review Theede 1963, Widdows & Bayne 1971, Widdows 1973, Schulte 1975, Bayne 1976, Hawkins et al. 1985). However, experiments with *Cerastoderma edule* (Loo & Rosenberg 1989) and *Ostrea edulis* (E. M. Rödström, Tjärnö Marine Biological Laboratory, pers. com.) show that filtration ceases at temperatures below 3°C. For *Hiatella arctica* (Ali 1970) filtration down to 1.5°C has been shown. For *M. edulis,* Jørgensen et al. (1990) have demonstrated filtration activity down to 2°C, and shown that the pumping rate increased with temperature, linearly correlated with the decrease in viscosity related to higher water temperature at a constant salinity.

Most experiments with bivalves performed so far have been conducted at temperatures of 5-17°C (Theede 1963, Widdows & Bayne 1971, Thompson & Bayne 1972, Vahl 1973, Widdows 1973, Winter 1973, 1977, Schulte 1975, Bayne 1976,

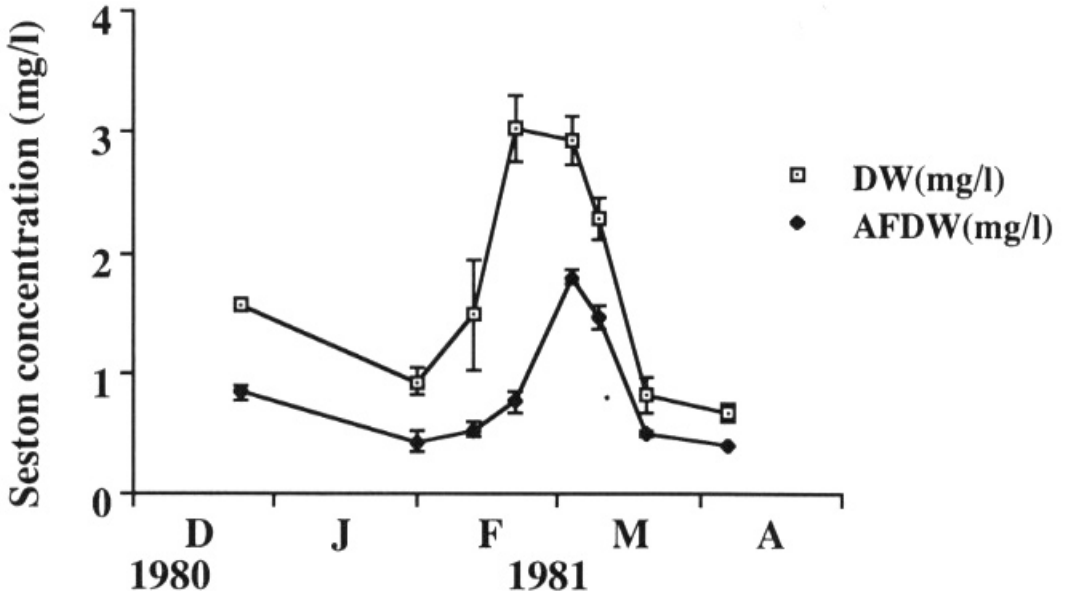

Fig. 2. Mean seston concentration during the spring-bloom. DW = dry weight (mg l^{-1}); AFDW = ash free dry weight (mg l^{-1}). Vertical bar: standard deviation (SD).

Møhlenberg & Riisgård 1979, Riisgård & Møhlenberg 1979, Widdows et al. 1979, Kiørboe & Møhlenberg 1981, Kiørboe et al. 1981, Riisgård & Randløv 1981, Hawkins et al. 1985). In this study, however, filtration activity was recorded for *M. edulis* down to -1°C. Salinity was 27‰ and sea water freezing point -1.46°C. Consequently, it is possible that *M. edulis* can filtrate at even lower temperatures than -1°C. There are however no possibility of quantifying the maximum ingestion because the experimental conditions were not fully compatible with undisturbed feeding. In this kind of experimental design, undisturbed mussels have earlier been shown to clear the water flowing through the tubes at rates that increase with water flow until a level is reached (Riisgård & Møhlenberg 1979), where recirculation of the water becomes insignificant. This pattern did not apply in my experiments where natural amount and composition of seston and several individuals of mussels were used. The amount of seston was in the same range as in earlier experiments by Riisgård & Møhlenberg (1979), who used a monoculture of phytoplankton. The variation between samples, however, might have been higher in my study. The temporal and individual variation in feeding activity was high during these low temperatures in the whole range of flows (Fig. 3), which may provide variable relationships between flow and ingestion rates. A parallel experiment (own results), with an instrument which registered the movements of the exhalant water, was carried out on the same group of mussels. The experiment showed that some mussels pump at maximum rate for a long time and then decrease drastically while some mussels pump periodically between maximum and minimum rate. There was no regular pattern in the pumping activity of the mussels.

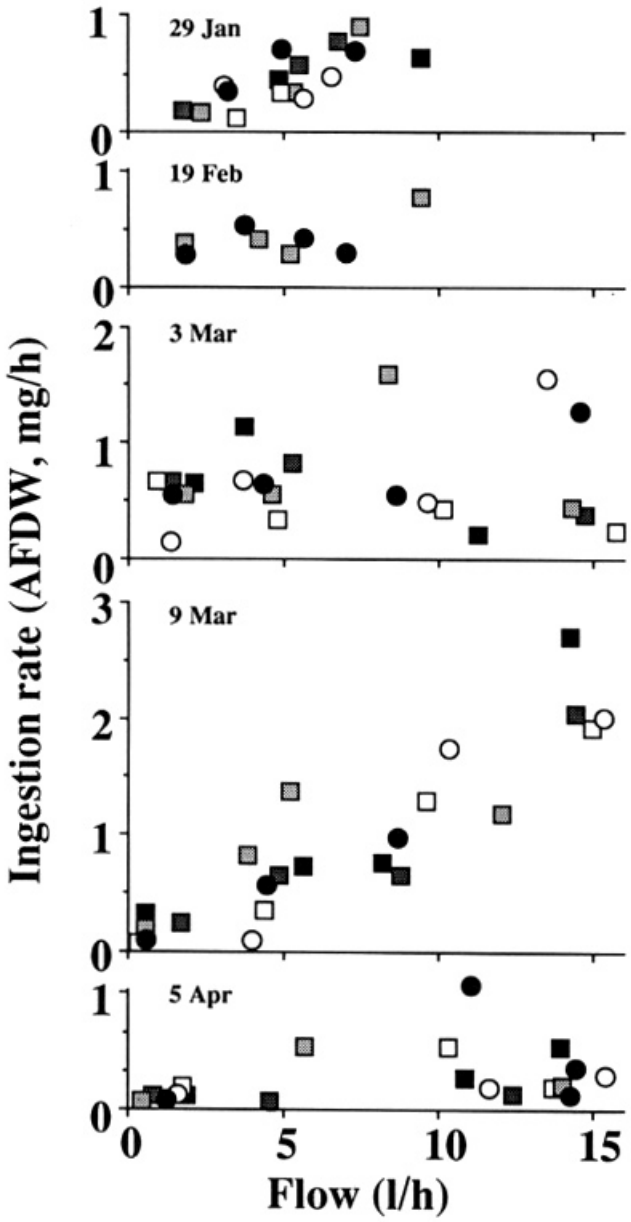

Fig. 3. Ingestion rate as a function of flow rate in the experimental tubes at five different occasions in 1981. Each of the six symbols in the diagram represents one mussel.

Absorption efficiency

Absorption efficiencies of *M. edulis* reported here for the spring-bloom period at low temperatures were within the range reported by other authors at higher temperatures (review, Bayne 1976). Hawkins et al. (1985), however, determined the absorption efficiency of *M. edulis* to 38% at about 5°C, compared to a range of 53-81% in this investigation. The higher absorption efficiency in this study may well be a result of the food quality during the spring-bloom. Thus, food quality could be a factor of great importance for assimilation even at low temperatures. Navarro & Winter (1982) have shown that absorption efficiency is independent of body size in *Mytilus chilensis*.

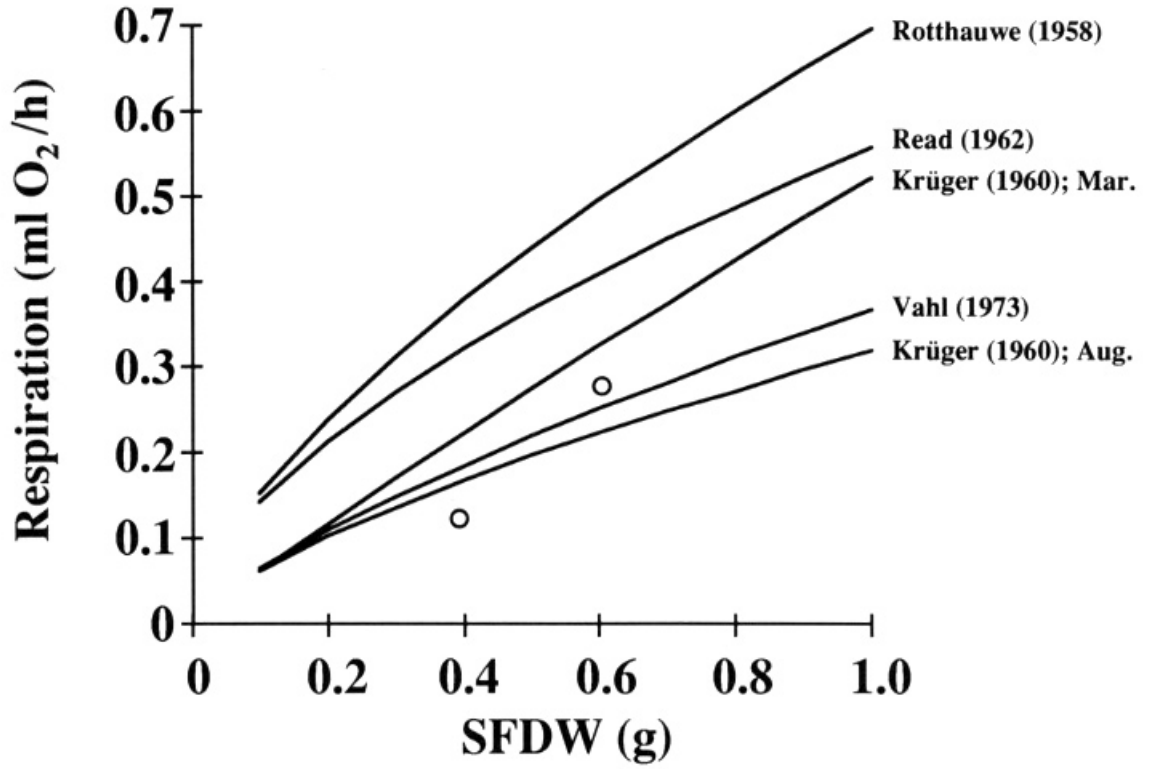

Fig. 4. *Mytilus edulis* respiration rates (ml O_2 h^{-1}) per SFDW (g). After Krüger (1960, March and August, 15°C), Read (1962, 3°C), Rotthauwe (1958, 16°C) and Vahl (1973, 10°C). The open circles represent the lowest and highest respiration rates during the experimental period.

Respiration

Respiration rates of *M. edulis* at low temperatures during this experiment were low compared to those reported by other authors (Fig. 4). Widdows et al. (1979) determined the influence of acclimation to different temperatures on oxygen consumption, filtration rate and absorption efficiency, albeit the lowest temperature used was 8°C.

Few measurements of respiration are recorded below 5°C. Some authors have done experiments around 5°C e.g., Bayne (1976), Hawkins et al. (1985) and Widdows & Bayne (1971). However, respiration measurement at low temperatures has been carried out on blue mussels in the Baltic Sea (Kautsky & Wallentinus 1980) at a temperature of -0.2°C, 0.06 mg O_2 g^{-1} h^{-1}, and on a cell-free homogenate of *M. edulis* at 1°C (Newell & Pye 1970). Respiration rate at the lowest temperature in my investigation (-1°C) was 0.14 ml l^{-1}.

Growth

Not so many field investigations have been done on growth of *M. edulis* at low temperatures. Loo & Rosenberg (1983) found no limiting effect of low temperatures during the spring-bloom 1979, where growth rate was high and the biomass of *M.*

edulis became doubled during the spring-bloom. At temperatures around 0°C Wallace (1980) has reported similar results from northern Norway, Thompson (1984) from Canada and Kautsky (1982) from the Baltic.

The specific growth rates of *M. edulis* reported by Loo & Rosenberg (1983) were 0.5% per day during the same time of year as in this study. These results were based on a mean growth rate for mussels in culture which is not an optimal feeding situation for all individuals. But in the present study all the individuals were exposed to an unused seston amount and the specific growth rate was then higher, 0.7% per day. No other growth data at such low temperature has previously been reported.

Conclusion

The conclusion of this investigation is that *M. edulis* has the ability to utilize the excessive amount of food produced during the spring-bloom. Consequently, a significantly limiting factor for the growth of *M. edulis* is most likely the availability and quality of food. Low temperatures are of secondary importance.

REFERENCES

Ali, R. M., 1970. The influence of suspension density and temperature on the filtration rate of *Hiatella arctica*. - Mar. Biol. **6**: 291-302.

Bathmann, U. V., T. T. Noji & B. von Bodungen, 1990. Copepod grazing potential in late winter in the Norwegian Sea - a factor in the control of spring phytoplankton growth? - Mar. Ecol. Prog. Ser. **60**: 225-233.

Bayne, B. L., 1976. Marine mussels: their ecology and physiology. - Cambridge University Press, Cambridge, London, New York, Melbourne. 506 pp.

Conover, R. J., 1966. Assimilation of organic matter by zooplankton. - Limnol. Oceanogr. **11**: 338-345.

Hawkins, A. J. S., P. N. Salkeld, B. L. Bayne, E. Gnaiger & D. M. Lowe, 1985. Feeding and resource allocation in the mussel *Mytilus edulis:* evidence for time-averaged optimization. - Mar. Ecol. Prog. Ser. **20**: 273-287.

Jørgensen, C. B., P. S. Larsen & H. U. Riisgard, 1990. Effects of Temperature on the Mussel Pump. - Mar. Ecol. Prog. Ser. **64**: 89-97.

Kautsky, N., 1982. Growth and size structure in a Baltic *Mytilus edulis* population. - Mar. Biol. **68**: 117-133.

Kautsky, N. & I. Wallentinus, 1980. Nutrient release from a Baltic *Mytilus*-red algal community and its role in benthic and pelagic productivity. - Ophelia, Suppl. **1**: 17-30.

Kiørboe, T. & F. Møhlenberg, 1981. Particle selection in suspension-feeding bivalves. - Mar. Ecol. Prog. Ser. **5**: 291-296.

Kiørboe, T., F. Møhlenberg & O. Nøhr, 1981. Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. - Mar. Biol. **61**: 283-288.

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

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

Loo, L. O. & R. Rosenberg, 1989. Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. - J. Exp. Mar. Biol. **130**: 253-276.

Møhlenberg, F. & H. U. Riisgård, 1979. Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves. - Mar. Biol. **54**: 143-147.

Navarro, J. M. & J. E. Winter, 1982. Ingestion rate, assimilation efficiency and energy balance in *Mytilus chilensis* in relation to body size and different algal concentrations. - Mar. Biol. **67**: 255-266.

Newell, R. C. & V. I. Pye, 1970. Seasonal changes in the effect of temperature on the oxygen consumption of the winkle *Littorina littorea* (L.) and the mussel *Mytilus edulis* L. - Comp. Biochem. Physiol. **34**: 367-383.

Read, K. R. H., 1962. Respiration of the bivalve molluscs *Mytilus edulis* L. and *Brachidontes demissus plicatus* Lamarck as a function of size and temperature. - Comp. Biochem. Physiol. **7**: 89-101.

Riisgård, H. U. & F. Møhlenberg, 1979. An improved automatic recording apparatus for determining the filtration rate of *Mytilus edulis* as a function of size and algal concentration. - Mar. Biol. **52**: 61-67.

Riisgård, H. U. & A. Randløv, 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. - Mar. Biol. **61**: 227-234.

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

Rotthauwe, H. W., 1958. Untersuchungen zur Atmungsphysiologie und Osmoregulation bei *Mytilus edulis* mit einem kurzen Anhang über die Blutkonzentration von *Dreissena polymorpha* in Abhängigkeit vom Elektrolytgehalt des Aussenmediums. - Veröff. Inst. Meeresforsch. Bremerhaven **5**: 143-159.

Schulte, E. H., 1975. Influence of algal concentration and temperature on the filtration rate of *Mytilus edulis*. - Mar. Biol. **30**: 331-341.

Theede, H., 1963. Experimentelle Untersuchungen über die Filtrationsleistung der Miesmuschel *Mytilus edulis*. - Kieler Meeresforsch. **19**: 20-41.

Thompson, R. J., 1984. Production, reproductive effort, reproductive value and reproductive cost in a population of the blue mussel *Mytilus edulis* from a subarctic environment. - Mar. Ecol. Prog. Ser. **16**: 249-257.

Thompson, R. J. & B. L. Bayne, 1972. Active metabolism associated with feeding in the mussel *Mytilus edulis* L. - J. Exp. Mar. Biol. Ecol. **9**: 111-124.

Vahl, O., 1972. Efficiency of particle retention in *Mytilus edulis* L. - Ophelia **10**: 17-25.

Vahl, O., 1973. Pumping and oxygen consumption rates of *Mytilus edulis* L. of different sizes. - Ophelia **12**: 45-52.

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

Widdows, J., 1973. The effects of temperature on the metabolism and activity of *Mytilus edulis*. - Neth. J. Sea Res. **7**: 387-398.

Widdows, J. & B. L. Bayne, 1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. - J. mar. biol. Ass. U.K. **51**: 827-843.

Widdows, J., P. Fieth & C. M. Worrall, 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. - Mar. Biol. **50**: 195-207.

Winter, J. E., 1973. The filtration rate of *Mytilus edulis* and its dependence on algal concentration measured by a continuous automatic recording apparatus. - Mar. Biol. **22**: 317-328.

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