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a distribution and population model of **mytilus edulis** in lake Grevelingen

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J. H. G. Verhagen

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PREFACE

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PREFACE

The research described in this report is carried out within the framework of WAter BASIn Model (WABASIM). WABASIM is organized as a multidisciplinary coproject of the Environmental Division of the Delta Department (DDMI) and the Environmental Hydraulics Branch of the Delft Hydraulics Laboratory (DHL), and is financed by the Delta Department.

The project aims at the development of aquatic ecological and water quality models, which can serve as tools in providing adequate guidelines for environmental management in the (future) water basins in the Delta area.

This report describes the development of a model for growth, mortality and distribution of the mussel Mytilus edulis in Lake Grevelingen. Special attention has been given to the description of the causal relation between the dynamics of the mussel population and external controlling factors.

The research and reporting is carried out by Ir. J.H.G. Verhagen.

The research activities are executed in cooperation with the WABASIM-salt project group, in which next to members of DDMI and DHL, also members of the Delta Institute for Hydrobiological Research (DIHO) participate. The WABASIM-salt project group consists of the following members (till Oct. 1983):

Ir. S. van de Kamer (DDMI), chairman
Drs. I. de Vries (DHL), secretary
Drs. C. Bakker (DIHO)
Dr. B. van Eck (DDMI)
Drs. P. Kelderman (DIHO), till September 1983
Dr. M. Knoester (DDMI)
Ir. R. Klomp (DHL)
Drs. R.H.D. Lambeck (DIHO)
Dr. H.J. Lindeboom (DIHO)
Ing. J.H.M. van der Meulen (DDMI)
Dr. P. Nienhuis (DIHO)
Drs. A.C. Smaal (DDMI)
Ir. J.H.G. Verhagen (DHL)
Drs. M. Veul (DHL), till June 1983

1 Introduction

This report describes the development of a model for growth, mortality and distribution of the common mussel Mytilus edulis in Lake Grevelingen.
In order to obtain ultimately a model applicable as a predictive tool for lake management, special attention has been given to the description of the causal relation between the wax and wane of the mussel population and external controlling factors.

The ultimate objective of the model development is to obtain a submodel of the macrozoobenthos which is one of the most important components of the Grevelingen foodweb.
At the time of the development of this one species model the abundance of the mussel population was such that it could be considered as representative for the higher aggregation level of the total macrozoobenthos group.
Due to the increasing abundance of other species in later years this presupposition appeared to be less appropriate.
The new situation has resulted in an apposition of the planning with respect to bottom fauna modelling within WABASIM-salt.

2 The controlling factors in the distribution of **Mytilus edulis** in Lake Grevelingen

The distribution of the mussel Mytilus edulis in Lake Grevelingen seems to be controlled by several factors. In this paper we try to get an impression of the relative importance of these factors and of the quantitative effect of each factor on the distribution.
The possible controlling factors are:

1. Limited availability of substrata suitable for the firm attachment of young mussels after settlement.
2. The magnitude of the current velocity above the bottom. Neither too weak nor too strong currents are optimal for the development of a mussel bed.
3. Wind-generated waves can agitate the bottom sediment especially during severe storms in such a way that young musselbanks, grown up there during the quiet period between storms, are destroyed.
4. Not only the water currents but also the food concentration in those currents controls the development of a musselbed. In fact the basic assumption made in this study is that musselbeds are located there where the food transport due to horizontal currents and vertical mixing is maximal.
5. Structural instabilities in the development of a musselbed.
6. Mussels do not occur on those places where the benthic boundary layer becomes permanently, or even temporarily anaerobic.
7. The mussel larvae need probably a fair amount of light during the time of attachment.
8. Interspecific competition for space.
9. The intensity of predation varies largely from one place to another and can be a controlling factor in the distribution of mussels.

The method used in estimating the relative importance of the various factors mentioned above is as follows.

The effect of each factor is quantified as good as possible. The estimated distribution of mussels controlled by that factor alone is compared with the measured distribution. The factor, which explains the nature of the measured

distribution to the greatest extent is marked as the most important one.
The differences between measured and explained distribution are analyzed, and the factor, which explains the largest part of the differences ranks on the second place in importance and so on.
Consider at first the suitable substrate limitation factor.

2.1 Limited availability of suitable substrata

This is undoubtedly the most quoted factor in literature thought to be responsible for the remarkably patchy distribution of musselbeds found in nature. As an example we may quote the results of a study made by Maas Geesteranus (1942) who showed that young mussels settle on all types of substrata, providing these were firm and had either a rough or discontinuous surface. He also showed that plantigrades attached and detached themselves many times before finally arriving at the established bed. The byssus threads seemed to be particularly important in providing a suitable substratum. Apparently it is assumed that outside the established musselbed locations the bottom is unsuitable for attachment. In this way the patchy distribution is in fact explained as a direct result of a limited availability of substrata suitable for the firm attachment of young mussels.
Although this controlling factor is probably important in open estuaries and in coastal waters, the importance in the closed Grevelingen seems to be rather limited. In fact a clear relation between substrate characteristics and mussel habitats in Lake Grevelingen has never been found. Therefore I left this factor out of discussion as long as possible during this study.

The next controlling factor in the distribution of musselbanks mentioned in the list concerns the magnitude of the current velocity.

2.2 The magnitude of the current velocity

The importance of currents on local distribution has received rather restricted attention in literature. It was mainly Verwey (1952) who stressed the importance of this factor in the Dutch Waddenzee.
Also in my study it appeared, that the distribution in the magnitude of the currents above the bottom could indeed explain a large part of the measured

density distribution of mussels in Lake Grevelingen.
The relation between the mussel biomass B in gram dry flesh weight per square meter and the velocity say one meter above the sediment-water interface, denoted by ub is calculated in this paper. The calculation is based on a population model to be described in the next sections and on the use of the conservation law of particulate matter.
The results of computer simulations showed that the annual mean value of B under steady-state conditions is more or less proportional to the bottom current ub. So, if the currents, say one meter above the bottom, were known the distribution of the mussel density controlled by this factor alone could be calculated.

In order to obtain the horizontal water velocity about one meter above the bottom a calculation of the wind-driven currents in Lake Grevelingen has been carried out by the Delft Hydraulics Laboratory. See G.J.H. Lindijer (1981). Those currents have been calculated using a three-dimensional semi-analytical steady-state model, to so-called Ekman-type model.
The result of such a calculation for a westerly wind is shown in figure 1. Depicted is the vector field of the horizontal velocity as integrated over the waterdepth.
It appeared from these calculations that the pattern of wind-driven circulation in Lake Grevelingen is dictated in the first place by the pronounced bottom geometry consisting of deep gullies (10-35 m) and a large shallow area (0-4 m). See Figure 2. To a lesser extent the pattern is influenced by wind direction. The prevailing direction of strong winds in the Netherlands is West-South-West.
Initially we will limit ourselves to a very global analysis of the results of such calculations. In doing so we observe that the vertical distribution of horizontal velocities has a parabolic shape. Observing that the velocities at the bottom are zero and that at the water surface the velocities have more or less the same order of magnitude everywhere, we conclude that the current velocities one meter above the bottom are more or less inversely proportional to the square of the local waterdepth.
So

$$u = C \cdot H^{-2}$$

where C is a constant and H is the local waterdepth.
Combining this result with the previous one we obtain the following relation between the mussel density and the local waterdepth:

$$B = \text{const.}\ H^{-2}$$

The theoretical result can be compared with measured data presented by Wolff et al. (1975), see Figure 3. The data given in this figure show that the zoobenthos biomass indeed decreases with depth. The rate of decrease however is somewhat faster than explained by the effect of currents alone. The differences have to be explained as the effect of other controlling factors listed at the beginning of this chapter.
The differences are:

- the zoobenthos biomass at greater depth is lower than explained, and
- the zoobenthos biomass in shallow water less than about 4 meter increases with depth instead of the explained decrease. The data show namely a maximum biomass at a depth of about 4 meter.

The first mentioned difference is ascribed to the effect of anaeroby in the benthic boundary layer, see 2.4.
The last mentioned difference is explained as the effect of storms which is item 3 in the list of controlling factors.

2.3 The effect of storms

The detrimental effects of storms on musselbeds are often reported in literature. As an example we may quote the observations of Verwey (1952), who states: "There are also localities in the Waddenzee, where old mussels are absent, but where conditions are quite suitable for the settling of young brood. On those places thousands of young mussels of one and the same size may grow out to extensive patches of some thickness. They may well be on the way to become true musselbeds when storms come and most of these patches are rolled up by the action of waves and currents and their mussels are carried away. The main reason for their destruction certainly is that these beds are

situated in most exposed positions; they can, therefore, grow up in quiet periods, but are destroyed again in stormy ones.
So, we cannot say that young mussels do not form beds, but the beds they form are destroyed. The mussels, which formed them, will gradually contribute to the importance of old beds, which chiefly grow through the addition of somewhat larger animals".

These observations of Verwey correspond to observations of Lambeck from the Delta Institute for Hydrobiological Research made in Lake Grevelingen. Lambeck measured in March 1980 a good recruitment of young mussels at some shallow location, depth 1.75 m. The mussels at this location originated from the 1979 year class. Two months later he found that these mussels were totally vanished. The weather synopsis of KNMI reports a southwestern storm along the Dutch coast on 28 and especially 29 March 1980 (daily-averaged velocity on 29 March at Vlissingen is 12.5 m/s).

Another interesting example of the detrimental effects of storms on musselbanks can be presented, by observing data from Wolff et al (1977) on the density of mussels as a function of time over a number of years (1972-1975).

The sampling location named Archipel is situated in the western part of Lake Grevelingen. The station has a sandy bottom at 3 m waterdepth and the area is to a large extent exposed to the wind. See Figure 4.

As can be seen from the figure the density in numbers of individuals per square meter show on several occasions a severe reduction between successive sampling dates. The reduction amounts even to an order of magnitude of a factor 25!

In trying to explain the reasons for this particular behaviour I found that the timing in the severe reductions during the years of observation coincides with the occurrence of severe storms. Table 1 shows the dates of the most severe storms at the South West coast during the period 1972 up till 1982. The data are taken from the weather synopsis of KNMI.

Table 1

2 April 1973
9-11 February 1974
25 November 1974
3 January 1976

The coincidence of both trains of events is too good to be accidental. See Figure 4.

The answer to the question, how near to the water surface a musselbed can exist, depends on:

a) to what extent the area is exposed to the wind
b) the frequency of occurrence of storms.

Ad a. The western part of Lake Grevelingen is more exposed to the wind than the eastern part.

Ad b. According to Table 1 severe storms did not occur between 1976 and 1982. Therefore musselbeds in that period could develop unmolested in more shallow water than in the preceeding 5-year period.

More quantitative information to answer the question properly fails however. All what can be said is that due to the effect of storm the mussel density will decrease with decreasing waterdepth, in that depth region, where wind generated waves can damage musselbanks. Judging from the available data this depth region could well be 0-3 à 4 meter. Therefore the qualitative picture of the effects of both controlling factors current and waves together will be as shown in Figure 5.

2.4 The anaerobic benthic boundary layer

Consider now the effect of the controlling factor number 6 of the list.
The chance that the water layer adjacent to the bottom becomes temporarily anaerobic increases the greater the waterdepth. The chance depends also on the magnitude of the vertical mixing at the given location. Because the westerly part of the lake is more exposed to wind, the chance of an anaerobic benthic boundary layer occurring at a given depth will be less in the western, than in the more sheltered and therefore less turbulent eastern part of the lake.
The data given in Figure 3 are not specified to sampling location and are obtained with a random sampling technique. Therefore the figure gives only information on the biomass density averaged over the lake area. Averaged over

the lake area the decreasing sediment oxygen condition at depth will result in a faster decrease of biomass density at greater depth. It is observed from the figure that the effect at least qualitatively explains the data. Below a depth of about 20 meter the bottom is often anaerobic, setting a limit to the maximum depth of mussel occurrence.

Up till now the data on the biomass distribution over depth as averaged over the whole lake area are qualitatively explained using the controlling factors numbered 2, 3 and 6 in the list. Next we are trying to find the factors regulating the horizontal distribution.

2.5 The food transport to the musselbed

It appeared from this study that the principal controlling factor consists of a combination of the distribution in magnitude of bottom currents and the distribution of food concentration. In fact it is stated in item 5 of the list, that musselbeds are located there where the food transport to the bottom is maximal. This statement has, as far as I know, not been developed earlier in literature. It is one of the main new findings obtained during this study. In order to quantify the distribution of food transport to the sediment water interface covered with mussels over the whole lake area, several aspects have to be considered.
Those aspects are:

a) The relative importance of the various food transport contributions.
b) The wind-driven currents as calculated with the three-dimensional Ekman-type model and the shortcomings of this model in predicting the distribution of the currents about one meter above the bottom over the lake area. Those currents are of main importance in transport calculations.
c) The results of more accurate flow calculations for simple geometrical configurations and the important differences between convergent and divergent flows.
d) The fact that the benthic filter feeders are probably food limited.
e) The occurrence of circulation cells and its consequences on the mussel distribution.
f) The condition defining the optimal mussel density distribution.

g) The theoretical optimal mussel density distribution in some idealized flow configuration.

Taking all these aspects into account, what will be the theoretical horizontal distribution of mussels in Lake Grevelingen? Does the theoretical distribution correspond with the measured one?
Let us consider the various aspects.

2.5.1 The relative importance of the various food transport contributions

Consider the vertical transport of suspended particulate organic matter to a musselbed:
Denote the concentration of particulate matter in the water column at the point of observation by FA. FA will be a function of the distance to the bottom z and of the time t, and depends further on the coordinates of the observation point. At the sediment water interface that is to say for z=0 the value of FA will be less than in the water column because the mussels remove continuously particulate matter by filtering the water.
The vertical transport of FA to the sediment water interface consists of two contributions:

- a dispersive transport due to turbulent exchange of water masses with different particle concentration which can be written as

$$D \cdot \frac{\partial FA}{\partial z}_{z=0}$$

  where D is the vertical dispersion coefficient

- a transport due to settling of the particulate matter which can be written as

$$v.FA_{z=0}$$

  where v is the settling velocity.

The relative importance of both contributions can be estimated as follows: The vertical dispersion coefficient D is proportional to the wind-driven current velocity, which in its turn is proportional to the wind speed. The value of D under normal weather conditions is estimated as 50 m^2/day.

The value of the settling velocity v is estimated as 1 m/day (Zison et al, 1978). An estimate of the order of magnitude of the gradient $\frac{\partial FA}{\partial z}$ near the bottom can be

$$\frac{FA_{z=d}-FA_{z=0}}{d}$$

where d is a measure of the particulate matter boundary layer thickness, estimated as 1-2 meters. The value of $FA_{z=0}$ is estimated as 0.2-0.8 times $FA_{z=d}$. See Wildish et al (1979).

So, the vertical dispersive transport contribution is estimated as 5-40 times $FA_{z=d}$, while the transport contribution due to settling is estimated as 0.2-0.8 times $FA_{z=d}$. So the latter appears to be only about 2% of the former and will be neglected in the further calculations made in this study.

Because dispersive transport in flow direction is negligible in most mass transport problems, the advective transport along the streamlines in the current above a musselbed and the vertical dispersive transport perpendicular to the bed remain as the most important transport contributions. In fact the mean horizontal water velocity say about one meter above the sediment water interface is one of the most important parameters determining the food flux to the musselbed.

2.5.2 The wind-driven currents as calculated with the three-dimensional Ekman-type model

To obtain the distribution of horizontal currents over the whole lake area say about one meter above the bottom, a three-dimensional flow calculation has to be carried out.

As mentioned already this has been done by Lindijer of the DHL (1979) using a steady-state semi-analytical Ekman-type model. This model is valid for shallow lakes in which the neglection of the non-linear convective terms in the momentum equation is allowed. Such an approximation is justified if characteristic depth/length ratios are small, or more precisely, do not exceed order 10^{-2}.

The condition implies also that bottom slopes in flow direction may not exceed order 1%. This condition is not always satisfied in Lake Grevelingen, especially not at those locations where water is flowing from a gully to a shallow area or in a reverse direction. It is well-known that musselbeds are usually found just on those sloping bottoms. The applicability of the Ekman-type model for this specific purpose can therefore be questioned.

Lindijer (1979) investigated the effects of neglecting non-linear terms on the model results in this application. He found that the large scale flow pattern can be considered free of convective effects and those results are therefore at least qualitatively reliable. More detailed results, however, as for instance the pattern of currents one meter above the bottom are considered as unreliable.

That is the reason that Figure 1 shows only the flow pattern averaged over the vertical and not the pattern of bottom currents.

What can be observed from the figure is that the circulation pattern in Lake Grevelingen is dictated primarily by the pronounced bottom geometry of deep gullies (10-35 m) and a large shallow area (0-4 m). See Figure 2. Simulation experiments showed that the pattern is influences to a lesser extent by wind direction. The prevailing direction of strong winds in the Netherlands is West-South-West.

From the calculated velocity field the pattern of wind-driven circulation is obtained as shown in Figure 6. It can be observed that several short closed circulation circuits exist. The exchange of water between neighbouring circulation cells will be less than within one cell.

The difficulty in obtaining a reliable picture of bottom currents brings again the question to the front;

Why are we exactly interested in currents about one meter above the bottom? Is it not enough to have a picture of the depth-averaged currents?

The answer is that we are interested in the vertical transport of particulate matter at the sediment water interface covered by mussels. More precisely, we are interested in the distributions of those places where maximum mass flow rates will be reached. The vertical transport is regulated by horizontal advection and vertical diffusion. From hydrodynamic theory it is known, that a high vertical transport of a substance to a horizontal wall corresponds in general to a small boundary layer in the concentration distribution of that substance. In that case the maximum food flow rate will be reached there where the vorticity generated by the musselbed in a current is confined to the neighbourhood of the bottom covered by the mussels. Such a situation occurs only if the fluid velocity near the bottom is continously increasing in the stream direction. This is the case in a converging flow where the volume flux is more concentrated at the region near the wall than it is in a diverging or even parallel flow.

Therefore Mytilus communities are found on gently sloping bottoms in a converging flow.

2.5.3 The results of more accurate flow calculations for simple geometrical configurations and the important differences between convergent and divergent flows

The large differences between convergent and divergent flows can only be described by a model based on the momentum equation including the non-linear convective terms. Because those differences are very important for our study, it is worthwhile to consider some results of more accurate flow calculations carried out in literature for more simple flow configurations.

The steady flow with a constant diffusion coefficient, in a -two-dimensional converging or diverging channel as a function of the angle between the walls and the Reynolds number has been studied by several investigators. The reader is referred to Batchelor (1967) p.p. 294-302 for a clear treatment of this fundamental hydrodynamic problem.

Batchelor's results are summarized in Figure 7. The angle between the walls is denoted by $2.\alpha$, where positive values of α correspond to diverging and negative values to converging channels. The symbol R stands for the local Reynolds number. As can be seen from the figure the effect of decreasing α to more negative values, or in other words, increasing the convergency of the flow, is to produce a flatter flow profile at the center with steep gradients near the wall. The effect of increasing α, which means increasing the divergency of the flow, is to concentrate the flow at the center of the channel. When the value of $\alpha.R$ exceeds 10.31, then even a region of backflow near the walls exist. The critical value $\alpha.R = 10.31$ corresponds with zero wall stress.

What is the meaning of these results for our mussel distribution problem? If the walls of the channel were covered with mussels, the critical value of $\alpha.R$

would mean, that the mussels were ventilating in water without a net current. Any food present in the boundary layer near the wall will be quickly removed by the filtering mussels, while any supply of food by advective transport fails to arrive. Therefore the mussels in such a channel remain nearly deprived of food supply and will not survive.

The critical value $\alpha.R = 10.31$ for the Grevelingen situation corresponds to a downward sloping bottom in flow direction with a slope $\alpha = 10.31/R$. An estimate of the turbulent Reynolds number is:

$$R = (U.H)/D = 400$$

based on the estimates $U = 4000$ m/day, $H = 5$ m, and $D = 50\ m^2$/day.

This value gives a bottom slope of 2.5%, which is a quite normal value at those locations where water is flowing from shallows into gullies. At those locations mussels will therefore never occur.

Because velocity gradients and therefore concentration gradients of food near the walls are steeper in convergent flows compared to parallel or divergent flows, the conclusion is that musselbeds are preferring sloping bottoms of several per cents in a converging flow.

2.5.4 The fact that the benthic filterfeeders are probable food limited

All of the foregoing considerations are relevant only if the filterfeeders and more special Mytilus edulis, being the main species in this group, are really food limited.

It is the outcome ofthe carbon cycle study carried out already for more than ten years by the Delta Institute for Hydrobiological Research that a not unimportant part of the net primary production by phytoplankton and microphytobenthos is consumed by the benthic macrofauna which mainly consists of filterfeeders. It may therefore be assumed that in general the benthic filterfeeders are food limited.

This assumption is even more justified if we realize ourselves that consumption and production of food occur in different parts of the lake. Namely, consumption occurs at musselbanks distributed apparently at random near the bottom all over the lake area, while production occurs only in the euphotic zone of the water column. Only about 6% of the bottom area is covered with musselbeds. In such a case the hydrodynamic transport rate between the different regions can also play a role as a limiting factor in the growth of mussels. An additional argument is the fact that the dry flesh weight/shell length ratio for the mussels in Lake Grevelingen is low as compared to average values reported in literature.

2.5.5 The occurrence of circulation cells and its consequences on the mussel distribution

Already we pointed out to the reader the occurrence of closed circulation cells in the calculated vertical averaged flow pattern of Lake Grevelingen. In order to check its consequences on the distribution of mussels, we consider the hypothetical case of no water exchange between those circulation cells.
Optimum food utilization implies that the primary produced material in each cell has to be consumed by the benthic filterfeeders which must be present in the same circulation cell, because there is no water exchange with neighbouring cells. Therefore, each circulation cell must at least contain one musselbed. In reality there is an exchange of water and hence of food between cells.
If the exchange rate of water from a cell is small compared to the relative production rate of organic matter then the foregoing reasoning remains valid. The reason is that the organic matter produced per unit time in a cell without mussels is not transported at the same rate by water exchange out of the cell and therefore decays unutilized as musselfood. The exchange rate of water between cells in Lake Grevelingen is estimated as 0.3/day. The relative production rate of organic matter in the growing season is estimated as 1.0/day, which is indeed faster than the exchange rate.
So, every circulation cell contains at least one musselbed.

2.5.6 The condition defining the optimal mussel density distribution

The vertical transport of food to the musselbed is equal to the product of the vertical concentration gradient of food and a vertical diffusion coefficient, both entities as measured at the musselbed. This hydrodynamic transport must be equal to the filtration rate of the mussel population per unit bottom surface, which can be written as the total ventilation rate of the stock per unit surface times the food concentration at the bed. So:

$$D \cdot \frac{\partial FA}{\partial z} = V_{filt} \cdot FA \qquad (1)$$

for z = z(bottom).

I stated in the beginning of this paper: Mussels are located there where the food transport to the bottom is maximal. This statement is not appropriate to determine the optimal mussel density distribution. The statements defining the optimal mussel density distribution should be:

The distribution of mussels affects the distribution of food in a lake. The mussels in Lake Grevelingen would have reached the optimal density distribution, if the yearly averaged food concentration at the bottom belonging to that specific mussel distribution has the same value at all those places where mussels can survive for reasons other than food availability.

The arguments leading to this statement are:
If the food concentration at a given location on the bottom, which is suitable for mussel attachment and survival, would be continuously higher than elsewhere in the lake, than mussels would occupy that location and grow faster then elsewhere due to the fact that growth is food limited, until the food concentration at that location is reduced to the same level as in other parts of the lake. Simular arguments can be given in the case of a location where food concentration is lower than elsewhere and where musselgrowth will lag behind until everywhere the same concentration is reached.
The distribution of mussels belonging to that situation is called the optimal distribution. "Optimal" because in such a situation there is no advantage for an individual mussel to move (if they were capable to) to another location. That mussel will filter the same amount of food per unit time at every location when using the same ventilation rate.

2.5.7 The theoretical optimal mussel density distribution in some idealized flow configurations

Would it be possible to calculate the optimal mussel density distribution in Lake Grevelingen?

The answer is that such a calculation only in theory could be carried out. There are two points which prohibit such an attempt. The first point is that the costs to develop such a numerical program together with the computer costs would highly exceed the economical value for the Dutch mussel fisheries.
The second point is the fact that the solution of the problem partly depends on poorly understood processes of recruitment and survival of young mussels. Therefore the value of the final result depends on the value of the specific assumptions of these processes made in the model.
It might be worthwhile to know what kind of submodels are needed to solve this problem. The submodels needed are:

1. A 3-D time dependent flow model based on the momentum equations including the convective terms.
2. A 3-D time dependent model of transport and production of musselfood, in which the consumption of food is incorporated by using the boundary condition at the bottom given by equation (1), where V_{filt} is still unknown.
3. A population model in which the ventilation rate of the mussel stock per unit bottom area, V_{filt} as a function of time, could be calculated, using the food concentration at the bottom as a function of time as a given input.

The last model contains the above mentioned weakly founded assumption on recruitment and survival of young mussels. The time needed to reach a stationary annual limit cycle solution from given initial conditions is dictated by the population submodel and is estimated to last 3 till 10 years.

At this stage it is more realistic to build up our understanding of the effects of the various parameters on the optimal mussel density distribution by using simple flow configurations and other simplifying assumptions. This has been done in Section 3. In the first example given in Section 3.1 the most simple flow configuration was used, namely a uniform steady flow parallel to the bottom. The steady-state mass transport equations in two dimensions along and perpendicular to the bottom, have been solved, using the boundary condition that FA is a given constant at the bottom. From the results the vertical turbulent transport to the bottom

$$-D \frac{FA}{\partial z_{z=0}}$$

as a function of x could be calculated.

This results in an optimal distribution $V_{filt}(x)$ depending on the given value of $FA_{z=0}$.
So: $(V_{filt})opt = F(FA_{z=0}, x)$.
Running the mussel population model for various levels of the annual cycling $FA_{z=0}$ until steady-state conditions are reached gives the annual mean V_{filt} as a function of the annual mean $FA_{z=0}$ and as a function of the prescribed annual recruitment.
So: $V_{filt} = G(recr, FA_{z=0})$.
Equating the two functional relations for V_{filt} at a certain value of $FA_{z=0}$ gives the annual recruitment as a function of the coordinate x, which is needed to achieve the optimal mussel distribution in numbers per square meter. At the same time the population model gives the biomass density distribution and therefore also the age-structure composition belonging to that optimal situation.

The described procedure in computation however has not been followed, because it is felt that not $FA_{z=0}$ but the annual recruitment is the real unknown. Therefore we started the calculation with a given annual recruitment and computed $FA_{z=0}$ belonging to it. It seems unrealistic to suppose that the calculated detail in density distribution, based on the crude assumption concerning the flow configuration, will correspond to reality. Therefore, we integrated the model results over the musselbed length and used only averaged values of mussel density and age composition per bed in further calculations.

A second approach is shown in Section 3.2. In this example a uniform flow in a circular channel is considered. The water velocity in this example is not a constant but varies in tangential direction inverse proportional to the varying waterdepth. Algae growing in the water at a constant relative rate or consumed by the mussels on the bottom. The optimal mussel density distribution is calculated using a simplified form of the mass balance equations. In fact the two-dimensional equations are written in a one-dimensional form using a two-layer model. For further detail see Section 3.2.

2.6 Structural instabilities in the development of a musselbed

A steady-state in the distribution of mussels seems to be never reached, even if environmental conditions would remain constant forever. This phenomenon arises from the fact that the development of a musselbed essentially contains instabilities.

For instance an old musselbank can be disrupted when the deposition layer of pseudo-faeces beneath the mussels become too thick resulting in a feeble attachment to a firm substratum.

Another example of bed instability mentioned in literature is due to competition for space in areas of fast growing mussels. Hummocking mussels have no direct contact with the substrate. Those mussels need long byssus threads to maintain their position, which result in a feeble attachment to one another. Many individuals fail in the competition for space.

The factor of structural instability seems to control the local irregularities in the mussel distribution. It is well-known that mussels occur in patches with a length scale of several meters within large beds several hundreds of meters long. There is always local concentration with areas without mussels in between. The question may be raised how such a patchy distribution can occur in an environment where the controlling factors as currents, suitability of substratum and distribution of planktonic mussel larvae are much more uniform or at least change only very gradually over the whole lake area. If recruitment was successful year over year and environmental conditions were favourable for mussel growth than it should be expected that young mussels, once settled, provided loci for further recruitment until the mussel population gradually covers the whole area without patches. The presupposition that recruitment is successful every year is however not fulfilled. Instead, a relation seems to be present between recruitment success and the age of the musselbed, as observed by Verwey (1952).

Verwey found in the Dutch Waddenzee that settlement of very young mussels on old beds is apparently limited, in comparison to settlement on young new ones. Such a mechanism, together with the mentioned instability in the development of beds can indeed be responsible for a considerable patchiness of mussels even in the final stage of development.

How to account for these instable processes in a simulation model?
At this stage a model as simple as possible is preferred. Incorporation of instable processes in a simulation model leads often to an unwieldy model. Therefore, I decided not to go into detail of local patchiness, but to consider only large scale variations in the distribution of variables. That means that the calculated density distribution is to be interpreted as the real density distribution averaged over an area of say one or a few hectares.

2.7 The effect of the last three items mentioned in the list of controlling factors

The effects of the need of light of mussel larvae, interspecific competition for space, and predation have not really been quantified in this study. On the one side, because relevant data are lacking, on the other side, because the data on mussel distribution could be explained reasonable well without any further opening of Pandora's box.

3 Modelling the food transport to the musselbed

In 1979 Wildish and Kristmanson presented a quantitative hypothesis that current velocity and roughness at the sediment water interface control the numbers, biomass and growth of suspension-feeding macrobenthic animals.
Although I do not believe that the intensity of spatfall is controlled by the mentioned physical factors and therefore reject part of the hypothesis, I fully agree with those authors, that the turbulent mass transport of food to the musselbed is one of the most important factors determining growth of the mussel community. In fact I used a comparable model formulation already for some time, being unaware of the previous attempts reported in literature. It was Dr. Bayne, who kindly drew my attention to the similarity between my approach and the work of these investigators.

Wildish et al (1979) used the following expression for the rate of mass transfer TR to the benthic suspension feeders:

$$TR = \gamma.ub.(FAIN-FA)$$

where ub the velocity say one meter above the sediment water interface, in m/s and γ a coefficient equal to about 0.003 depending on bottom roughness. FA refers to the concentration of particulate organic matter at the bottom, and FAIN to the concentration in the bulk of the water column.
In the present paper a somewhat different approach is followed leading to a quantitative comparable but qualitative more detailed result. The approach is as follows:
Consider a musselbed on a sloping bottom in a convergent wind-driven flow. See Figure 8.

The mean current velocity say one meter above the sediment water surface is denoted by ub and is pointing in an uphill direction. The distribution of the horizontal velocity over the water column outside the region near to the bottom might be of any shape in magnitude and direction. The length of the musselbed measured in the direction of ub is denoted by L.
The physical or biological factors determining the musselbed length are in fact quite unsure. It is believed that the factors determining the musselbed

length are related to bottom geometry and current properties.
For instance, it may be that the front side of the musselbed viewed in the direction of ub is fixed by the criterium that it is the deepest point where the bottom remains aerobic at every day of the year, or that it is the deepest point where the bottom is stable and hard enough to be suitable as a substrate for mussel attachment. The end of the musselbed is assumed to coincide with the top of the hill.
In the beginning of this paper we derived that the optimal mussel density distribution is reached when the concentration FA of particulate organic matter at the bottom does not vary along the musselbed.

3.1 First example of schematizing the flow

It is not realistic to assume that the time-mean value of ub is also constant along the musselbed. Nevertheless, we make such an assumption. Next we will integrate the solution of the mass conservation law over the length of the musselbed, hoping that the result is a reasonable approximation of averaged real values.
The suspended organic material in this example is considered as a conservative substance, with concentration c(x,z,t). In this section we use the short notation c instead of FA. Conservation of mass for a steady-state situation states:

$$ub \cdot \frac{\partial c}{\partial x} = D \frac{\partial^2 c}{\partial z^2}$$

Assume ub to be independent of the vertical coordinate z over the thickness of the mass boundary layer δ. Outside the mass boundary layer the concentration is assumed to be constant and equal to ci. So the boundary conditions are:

for $x = 0$ $\qquad c = ci$

$z = \infty$ $\qquad c = ci$

$z = 0$ $\qquad c = cb$

The solution of the conservation of mass law is:

$$\frac{ci-c}{ci-cb} = \operatorname{erfc}\left(\frac{z}{\sqrt{4Dx/ub}}\right)$$

and the mass transport directed towards the bottom at the location x is

$$T = +D\left(\frac{\partial c}{\partial z}\right)_{z=0} = -D(ci-cb)\,\frac{d}{dz}\,\operatorname{erfc}\left(\frac{z}{\sqrt{4Dx/ub}}\right)_{z=0}$$

$$= D(ci-cb)\,\frac{2}{\sqrt{\pi}}\sqrt{\frac{ub}{4Dx}}\,\exp\left(-\frac{z^2.ub}{4Dx}\right)_{z=0} = (ci-cb)\sqrt{\frac{D.ub}{\pi x}}$$

So the food transport to the musselbed is maximum at the front of the bed and decreases in stream direction proportional to $x^{-\frac{1}{2}}$. The consequence will be that the mussels at the front of the bed grow better and will become larger than at the rear of the bed. As already said, it is not realistic to suppose that ub is always constant. In fact, in reality ub may even change in direction from one day to another. Therefore we prefer to work only with averaged values over the length of the musselbed.
The mass transport equation averaged over L becomes:

$$T = (ci-cb)\sqrt{\frac{4D.ub}{\pi L}} \qquad (2)$$

Wildish D.J. and D.D. Kristmanson (1979) expressed the turbulent mass transfer of food to suspension feeders as:

$$T = \Upsilon.ub(ci-cb) \qquad (3)$$

where Υ is a dimensionless coefficient equal to $\approx 3.10^{-3}$ depending on bottom roughness.
The vertical dispersion D in equation (2) refers to the dispersion in the bottom region. According to mixing length theory the dispersion is:

$$D = u^*.\kappa.z$$

where z = distance to the wall = order (1 m)
κ = the Von Karman constant = 0.42
and u^* = the wall friction velocity defined as $u^* = \sqrt{\frac{\tau b}{\rho}}$

The bottom friction is $\tau b = Cd.\rho.ub^2$ where $Cd = 1.5.10^{-3}$ valid for a rough wall and $Re = 10^6$. The dispersion coefficient becomes:

$$D = 0.42 \;.\; z(\frac{\tau b}{\rho})^{\frac{1}{2}} = 0.42 \;.\; z\, C_d^{\frac{1}{2}} \;.\; ub$$

$$= 0.016\ ub$$

and equation (2) can be written as:

$$T = (ci-cb).ub.\sqrt{\frac{0.065}{\pi.L}} \tag{4}$$

An estimate of the length of a musselbed in Lake Grevelingen measured in the direction of the flow near the bottom is L = 2000 m. In that case T becomes:

$$T = (ci-ub)\;.\;ub\;.\;0.0032 \tag{5}$$

As can be seen the expressions (5) and (3) are quite similar for standard values of the musselbed length. However, equation (2) is preferred above equation (3) of Wildish because it expresses the effect of the musselbed length on the averaged vertical mass transport.

The transport of particulate matter to the bottom T is equal to the rate at which the water at the musselbed is cleared from particles. The latter rate is equal to the summation of the filtration rate of all the individuals per square meter. The filtration rate of one individual at the conditions at time t depends on the weight of that individual at time t.

In a population model with recruitment on a fixed data of the year and with neglection of differential growth between individuals of the same age class all the individuals of one age class have the same weight on a given day.

The summation over all the individuals reduces in that case to a summation over the filtration rate pro age class

$$N(i).v_{filt}(i).cb$$

The total filtration rate per square meter becomes:

$$T = \sum_{i=1}^{\infty} .N(i).v_{filt}(i).cb = V_{filt}.cb \tag{6}$$

Combining (4) and (6) leads to:

$$\sum_{i=1}^{\infty} .N(i).v_{filt}(i).cb = (ci-cb).0.144 \frac{ub}{\sqrt{L}} \tag{7}$$

This equation is a more elaborated version of equation (7) of Wildish et al (1979).

Using the model of Bayne et al as given in the next section, the mussel weight as a function of cb can be simulated and therefore $v_{filt}(i)$ also.

The unknown function cb can therefore be solved from equation (7) if N(i), ci, ub and L were given. The last three parameters can be considered as given input parameters in the model defining the environmental conditions at a specific musselbed location.

3.2 Second example of schematizing the flow

The optimal mussel distribution in the foregoing model has been calculated based on the assumption, that the velocity ub near the bottom did not vary in flow direction. From the discussions given in this paper it will be clear that our main interest is directed to convergent flows in which ub accelerates along streamlines. Therefore it seems appropriate to treat another situation, in which the flow configuration bears a somewhat better resemblance to the circulation cells as observed in Lake Grevelingen. Consider the following flow configuration. See Figure 9.

A circular channel is considered in which a steady water flow rotates.

The water depth of this channel is not constant. The bottom slopes up at one part of the circumference and slopes down at the other part. For reasons, related to boundary layer separation, as mentioned earlier in this paper, it is assumed that mussels do not occur on the down sloping bottom. In the region where the bottom slopes up it is assumed that the flow is uniform over the cross sectional area of the channel. So the water velocity in that part of the circuit is inverse proportional to the varying waterdepth.

Algae growing in that water at a constant relative rate are consumed by the mussels on the bottom. The optimal mussel density distribution is calculated using a simplified form of the mass balance equations. In fact the two-dimensional equations are written in an one-dimensional form, using a kind of two-layer approach.

Denote the depth mean concentration of algae as ci.

The consumption of algae by the mussels on the bottom per unit surface is written in the form given by Wildish et al. as:

$$\text{cons} = 0.003.\text{ub}.(\text{ci}-\text{cb})$$

where ub = u = Q/H the water velocity at location x.

The nett algae production per unit water surface is assumed to be proportional to ci, so

$$\text{prod} = H_0.\mu.\text{ci},$$

where H_0 is the depth of the euphotic layer and μ the relative net growth rate, both considered as being constant.

The mass balance equation for steady-state conditions becomes:

$$Q.\text{dci}/\text{dx} = H_0.\mu.\text{ci} - 0.003.\text{u}.(\text{ci}-\text{cb})$$

valid in that part of the channel where mussels occur, say $0 \leq x \leq L_1$.

At the remaining part of the channel, where $L_1, < x < L$ we have:

$$Q.\text{dci}/\text{dx} = H_0.\mu.\text{ci}$$

The solution of the last equation is an exponential growth function:

$$\text{ci} = c_0.\exp(\mu.H_0.(x-L)/Q)$$

where c_0 is the value of ci at x = 0, which must be equal to the value at x = L.

The first differential equation can be solved for given H and cb as functions of x.

We are interested in the optimal mussel distribution which occurs if:

cb is constant

Instead of prescribing H as a function of x, we prefer to prescribe the behaviour of the solution of the diff. eq. as a function of x and derive the corresponding depth-x relation.

Let the behaviour of the solution be:

$$ci = c_o + c_1.(1-\exp(\beta.x))$$

Substitution in the d.v. gives:

$$-Q.c_1.\beta.\exp(\beta.x) = ci.(H_o.\mu-0.003.u) + 0.003.u.cb$$

The water velocity u becomes:

$$u = (ci.H_o.\mu + c_1.\beta.Q.\exp(\beta.x))/(0.003(ci-cb))$$

and the waterdepth becomes:

$$H = 0.003.Q.(ci-cb)/(ci.H_o.\mu + c_1.\beta.Q.\exp(\beta.x))$$

which can be written as:

$$H = 0.003.Q.(c_o+c_1-cb-c_1.\exp(\beta.x))/((c_o+c_1).H_o.\mu+c_1.\exp(\beta.x).(\beta.Q-H_o.\mu))$$

The consumption rate of algae is:

$$cons = V_{filt}.cb = ci.H_o.\mu + c_1.\beta.Q.\exp(\beta.x) \text{ or}$$

$$V_{filt} = H_o.\mu.(c_o+c_1)/cb + (c_1/cb).(\beta.Q-H_o\mu).\exp(\beta.x)$$

Figure 10 and Figure 11 show some results.
The parameter values in both figures are:

Q = 20.000 m^2/day
u = 4000 m/day
H_o = 5 m
L_1 = 2000 m
L = 6000 m
μ = .5 1/day
cb = $c_o/3$
$\beta . L_1$ = .5 respectively .2 in figures 10 and 11.

Let us compare some results of the both examples given: calculated is the optimal distribution in filtration rate $V_{filt}(x)$ for two different flow distributions.
In example 1, the bottom flow was taken as constant. This resulted in an optimal filtration rate proportional to $1/\sqrt{x}$.
In example 2 the bottom flow was taken as an increasing function of x. The resulting optimal filtration rate could decrease or increase with x, depending on the gradient du/dx.
The first result shows that mussel density (or V_{filt}) decreases in downstream direction. This result is easily to understand, considering that mussels remove food from the water and as a result less food is left for those individuals living downstream of others.
Unless, as is shown in the second example, the supply of food by advective transport is fast enough increasing in downstream direction to compensate for this effect.

The summarized results show clearly, that the optimal mussel density distribution depends closely on the distribution of flow velocity near the bottom.
Real values of the latter could not be calculated for the Grevelingen Lake.
So we had to make a choice what kind of flow velocity distributions we want to base our mussel population model. For reasons of simplicity the choice of a constant u has been made. No further attention has been paid in this study to the optimal density distribution of mussels, inside a bed; belonging to this specific choice. In the population model only musselbed averaged values of numbers and biomass to age data will be used.

4 The population model

A simulation model is constructed which describes the production and development of a population of Mytilus edulis over a sequence of years. The development of the population expressed in biomass and numbers of individuals of subsequent year classes is followed from spat settled at day 105 on a bare bottom up till a nine year class mixed age population is reached. The weight on one just settled young mussel is taken as 0.3 mg dry flesh weight.
Growth, mortality and spawning weight loss for each age class are calculated as functions of external variables as temperature, season and food concentration in the water column away from the musselbed.
Those forcing functions are given in Figure 12.
The temperature was set equal to an annual cycle typical for the Grevelingen Lake. Also the concentration of particulate matter and the proportion of organic matter in the water column away from musselbeds were set equal to values recorded in the Grevelingen Lake. Recruitment if successful was given a prescribed density of 5.000 m^2 and zero if not successful. The controlling factors for recruitment success are discussed in the next section.

4.1 Recruitment

Recruitment appeared to be the most difficult process to predict.

4.1.1 The first approach

The first approach has been to describe the relation between the abundance of spawners and the number of subsequent recruits. A model based on this approach has been presented at the third ISEM conference, Fort Collins 1983. The behaviour of that model and a comparison with measured data will be given.

The model as given in the ISEM-paper calculates the fertile egg-production of the mussel population in terms of its age- and size-structure and abundance. The life cycle of the mussel is modelled in that paper by tracing survival and growth from the egg through larval stages to the recruit stage and adult stages. In fact the model describes in a detailed way the relationship between the abundance of spawners and the number of subsequent recruits.

The study of this relation has a long history in the research on exploited fish populations. See for instance Beverton and Holt (1957).
It seems illustrative to explain the behaviour of the ISEM-paper model in terms of the findings of earlier studies in the literature.

A well-known representation of the relation between egg-production and recruitment for specific fish populations is given in Figure 13.

The decline in recruitment at higher egg production is in the ISEM-paper caused by cannibalisme, i.e. predation of larvae by the adult mussels. The problems concerning the stability in the dynamics of those populations has been extensively studied in literature. The behaviour of the mussel population model given in the ISEM-paper shows that a single transitory change in environmental conditions such as those related to the closure of the estuary, set up self-induced oscillations in population abundance which would beer no obvious relation to subsequent environmental changes. The oscillations are of the same general type as those shown by the theoretical population model, introduced already by Hutchinson in 1948, as given in equation 8.
In that model the rate of change of numbers at any instant depends on the past history of the population abundance.

$$dN/dt = rN(1-N(t-T)/K) \qquad (8) \quad \text{See May (1956)}$$

The density dependent regulatory mechanism $1-N(t-T)/K$ in this equation operates not instantaneously, but with some built-in time lag T, whose characteristic magnitude is the mean generation time T. The mean generation time T is defined as

$$T = \sum_{x=1}^{n} \ell_x \cdot m_x \cdot x \,/\, \sum_{x=1}^{n} (\ell_x \cdot m_x)$$

x = age in years
ℓ_x = number of survivors at start of age x
m_x = number of eggs produced per female aged x per year
n = number of age classes

The sustained cycles of oscillations which can result from the model given by equation (8) have a periodicity of about 4T years. The mean generation time of a mussel population however is not a constant, but depends on the condition of the population. According to Bayne, who is presently studying this subject (personal communication), the mean generation time shifts significantly to younger ages for a population under stress conditions.

Is the described behaviour of the model in agreement with the available data on the mussel development in Lake Grevelingen?

The available data on the mussel development in Lake Grevelingen are insufficient to give a clear answer to the question of the correctness of the model behaviour. In this respect it has to be remembered that the presence of extremely large fluctuations in recruit numbers from other causes than population size would tend to obscure anything but a fairly pronounced relationship, unless data from a very long (at least several decades) series of years were available. Nevertheless there are indications that the model is unsuccessful in predicting recruitment success. These indications are:

1. Data on abundances of lamellibranch larvae as measured by Bakker from 1976 to 1980 give no grounds for the assumption that the low recruitment after 1977 is caused by low numbers of mussel larvae. The data of peak abundances in numbers per 100 L are:

First period	G 11	G total	West	Central	East
1976 - 26/4	30	-	-	-	-
77 - 25/4	2.000	1.700	2.000	17.000	600
78 - 8/5	400	940	1.200	700	750
79 - 24/4	250	-	-	-	-
80 - 28/4	250	495	790	250	214

Second period

1976 - 17/5	6.500	-	-	-	-
77 - 16/5	200	880	850	910	870
78 - 22/5	5.500	3.100	3.100	3.400	1.750
79 - 22/5	18.000	13.000	6.500	22.000	7.300
80 - 27/5	850	360	-	-	-

The first peak in abundancy of larvae at the end of April or in the beginning of May could possible be interpreted as being mussel larvae. The second peak measured in the second half of May could possible consist out of cockle larvae. Under normal conditions mussel larvae are indeed earlier in the year, but by food limitation the spawning can be delayed (Bayne). The settlement success as measured by Lambeck during the same years revealed that recruitment was very successful in 1976. The peak abundance of larvae in April 1976, however, was the lowest ever measures and in May 1976 high but not as high as those during the poor recruitment years 1978 and 1979.

2. The recruitment success depends on other factors than the abundance of larvae alone as is clearly demonstrated by data from Lambeck. Lambeck measured in March 1980 a good recruitment of young mussels at some shallow location in the lake (depth 1.75 m) originating from the 1979 yearclass. Two months later he found that those mussels were totally vanished!

The workshop devoted to the improvement of the population model as given in the ISEM-paper, held Sept. 2 1982 at Middelburg came to the conclusion that indeed the model as formulated can not explain the data. The factors introduced into the model to describe the recruitment success were however judged as the best possible seen from present state of knowledge. The main determining factor for the Lake Grevelingen situation has not yet been found.

Because this situation is very unsatisfactory the formulation as given in the ISEM-paper has been left and further study has been devoted to a search for possible factors determining recruitment success in Lake Grevelingen.

4.1.2 The second approach

The second approach is based on the suggestion made in literature, (Dare 1969, 1971, 1975), that settlement success may be controlled by physical and biological events on the musselbed themselves rather than on the availability of mussel larvae in the water column.

The opinion that mussel larvae are produced in excess for an optimal reproduction each year is based on the following arguments:

1. The mussel stock seven years after closure of the Grevelingen estuary is of the same order of magnitude as before the closure. Before the closure the largest part of the mussel larvae produced were lost to the North Sea. The remainingh larvae were still abundant enough to maintain the stock. So after the closure more larvae remain in the Grevelingen than before, which justifies the stated assumption.
2. It appears that no clear relation can be observed between larval numbers and the adult stock. Also other ecosystem studies (Wash estuary, Baltic Sea) were not successful in relating larval numbers and settlement success (Bayne).

The question which biological and physical factors control settlement success has not been solved. The biological factors as predation and infection are of course important in regulating recruit numbers but they are not expected to be decisive in the question concerning success or failure.

In this approach it is assumed that recruitment success is more dependent on physical factors than on biological ones. Mussel larvae are able to settle and detach themselves several times.
The final settlement will be on such a place where conditions are acceptable for the young mussel. These conditions are: suitable substrate and suitable food supply. An already existing musselbed satisfies in general these conditions. It is believed that the first day's or perhaps weeks are decisive whether the young mussel will stay on that location or not. If that is true than settlement success on a existing musselbed depends on the amount of food present above the musselbed at the time of final settlement which usually

occurs in July-August.
Recruits have to compete for food with mussels from the preceeding year classes, resulting in low food concentrations at the musselbed.
So the hypothesis is:
Settlement is unsuccessful if the food concentration at the musselbed in the critical period July-August (mainly August) is lower than a given value. If such a situation occurs than the young mussel will settle on other locations, which are not always suitable for an undisturbed development.

The stated hypothesis gives a possible explanation of the phenomenon observed by Verwey that settlement of young mussels on old musselbeds is very limited compared to young beds. A recruit can make a distinction between a young and an old bed, if it "measures" the food concentration at the bed. The food concentration at a young bed will be higher than at an old bed because the latter has reached the steady-state condition which is food limited.
If the food-limiting recruitment hypothesis is true, the important question can be raised by which external factors the recruitment is controlled?
The answer is, that it are those factors which influence the food supply to the musselbed in the critical period July-August. This food supply is proportional to the current velocity and hence to wind-speed. Further it is known that thermal stratification hampers the vertical transport considerable. So, the answer is, that recruitment to musselbeds in deeper water is controlled by the weather conditions during the period July-August. Sunny weather with low wind-speeds during this period will result in a poor recruitment especially in deeper parts of the lake.

The space limitation as a control factor in recruitment.
Much attention has been given to the effect of space limitation on recruitment. In literature a density dependent recruitment is often introduced. (See also the next section.) We tried several formulation to incorporate the aspects into the model. Those activities have produced results which did not really contribute to an increase in our insights. Therefore they are not reported. Besides, field data from the Grevelingen Lake show no systematic correlation between the number density of the 0 age class and the 1+ age class. So the importance of this factor on recruitment seems to be limited.

In the simulation model as it stands now it is assumed that the recruitment of plantigrades on to established musselbeds takes place on a fixed date.
This date is choosen to be day 210 + n.365 (n = 0,1,2,...). The assumption is rather crude. Further research is needed to find and quantify the controlling factors in the timing of settlement. Further it is assumed that recruitment is successful only if $FA > FA_{min}$ on day 210 + n.365 (n = 0,1,2,...).

4.2 Mortality

Annual mortality is a decreasing function of age class. Mortality is due to a large number of factors including physical factors such as storms, salinity, excessive silt and temperature, natural enemies as predators (crabs, starfish, birds), competitors for food and space, and parasites.
The decrease in numbers by mortality is:

$$dNi/dt = -Mi.Ni$$

Estimates of the age-dependent mortality rates thought to be reasonable, Bayne (personal communication), are:

Year class	Percentage annual mortality
0	80
1	60
2-9	40

These mortality rates are considered as density independent.

During this study much attention has been given to the formulation of a density dependent mortality factor due to the intraspecific competition for space. (See also the recruitment section). Initially the well-known model formulation was used that the mortality coefficient is linearly related to the population density, so it has been stated that:

$$dNi/dt = -(\mu_{1i} + \mu_{2i}.Ntot).Ni$$

The term μ_{1i} has the same meaning as the coefficient Mi in the foregoing expression, that is, it refers to the density independent component of the mortality, whereas the term μ_{2i} can be regarded as an interaction effect between individuals of the population. However, the foregoing formulation has been left after some time, because increasing evidence was obtained from several sources of literature that such a simple relation for mussels does not exist.

The problem of natural regulation of population-density is of fundamental importance and has been studied for more than a century. Two questions may be asked:

1. What stops population growth?
2. What determines average abundance? (The abundance in general show more-or-less restricted fluctuations). -

Three general theories answer these two questions.

- The biotic school suggest that density-dependent factors are critical in preventing population increase and in determining average abundance. Natural enemies and in the case of benthic animals like mussels and barnacles, space limitation are believed to be the main density-dependent factors.
- The climate school emphasizes the role of weather factors affecting population size. They suggest that weather may also act as a density-dependent control.
- The comprehensive school stresses that all factors are important, both density-dependent and density-independent ones and that population changes are controlled by a complex of biotic and physical factors varying in space and time.

The previous theories of natural control have concentrated on the role of the extrinsic factors in control: as food supply, natural enemies, weather, diseases and shelter.

Self-regulation through mechanisms going on within a population is not considered as a separate theory. It is assumed that those intrinsic factors are initiated by external stimuli.

During this model study, most of the factors suggested by the various schools

have been formulated in successive model versions. Numerical experiments with the various model versions has been carried out, giving insights into the full dynamic implications of the underlying assumptions.
We will report her some of the findings.

The density in numbers per square meter of a mussel population depends on recruitment and mortality. In the foregoing section we mentioned already the effect of some density-depenedent factors in the recruitment process which has been studies. We summarize here the factors active in the prerecruitment stage:

1. Cannibalism on larvae by adult mussels.
2. A reduction in egg production and quality dependent on the condition of the spawning mussel. (See the ISEM-paper.)

and the factors active in the post recruit stage:

3. Food limitation initiating emigration from the existing musselbed.
4. Space limitation.
5. Weather conditions.

The four first factors belong to the biotic school. The last factor belongs to the comprehensive school. Only the last two factors seem to be important in the Grevelingen Lake.
In this section we will discuss the effects of various factors controlling mortality in the post recruit stage.
Let us consider now the factors suggested by the various schools.

4.2.1 The biotic school

1. Space limitation.
   Griffiths (1981) found that $N.s^2$ is more or less constant for an one cohort population of the black mussel, Choromytilus meridionalis, where N is the carrying capacity in number of individuals per m^2 and s the size of an individual. So, she introduced in fact a mortality dN/dt which is inversely proportional to the rate of increase of s^2, i.e. the rate of increase in want of two-dimensional space.

On the other hand Kautsky (1982) found in the high density mussel population of the Baltic Sea that no density dependent mortality occurred. He observed that a large quantity of very small mussels (1-2 mm) was always present and did not grow at all. He called this a "waiting stage". An individual left the waiting stage and started to grow as soon as room became available by the dead of an old mussel. So, in fact mortality and recruitment to the adult population are in Kautsky's concept in permanent equilibrium. In other words the carrying capacity is always booked up.

If indeed, a density dependent mortality regulated the numbers of mussels per square meter in Lake Grevelingen than those numbers should be approximately constant in time, or show more or less regular oscillations. Grab samples taken at various locations showed however an enormous variation in the number density. Even at nearly the same location the variation in number density appeared at least an order of magnitude higher than the variation in biomass per square meter.

This observation suggests that the regulation in population density is active much more in biomass than in numbers. Density-dependent mortality, due to space limitation is therefore considered as less important in Lake Grevelingen.

2. Food limitation.

   It has been formulated in some model version, that mortality was a decreasing function of growth rate, which on its turn depends on the food supply. This model version reproduced the findings of Worrall (personal communication) that mortality increased especially during wintermonths, when mussels are loosing flesh weight. However, it has been left out of further consideration, after it turned out that the formulation resulted in a higher mortality of large mussels under food limiting conditions, compared to (non-food limited) smaller individuals. The model results showed therefore a shift to younger ages under food limiting conditions, which is considered less plausible for the Lake Grevelingen situation.

3. Predation.

   Quantitative estimates of the food consumption by starfish given in a DIHO's student-report D5 (1974) written by Van der Schoot, indicate that predation although important is unlikely to be the main factor in regulating numbers. The data are:

Predation by starfish:

in 1973 between 0.28 - 1.83 g/m^2
in 1974 between 0.16 - 0.65 g/m^2.

The biomass in those years was about 10 g/m^2. A P/B ratio of one or more is common (Wolff). So predation can not really explain the nearly complete loss of recruits in those years at the location named Archipel.
The effect of natural enemies on mussel mortality has not been considered in this study.
It must be mentioned that Lambeck of DIHO found an enormous increase of Nassarius reticulatus after 1976. He suggested that this animal could be responsible for the predation and severe loss of very young mussels after that year (Lambeck 1982).

4.2.2 The climate school

1. The detrimental effect of severe storms on musselbeds have been discussed already in Section 1.
2. Dispersal loss due to the effect of temporary stratification during the critical months July-August. It is assumed in this study that settlement is unsuccessful if the food concentration at the musselbed in those months is lower than a given value. Thermal stratification, even if lasting no longer than a few days, can promote such a condition. If such a situation occurs the young mussel will detache and will be dispersed by currents to places which are usual shallower and not always suitable for an undisturbed development. Many dispersed young mussels will not survive.

4.2.3 The comprehensive school

The factors mentioned by this school are a combination of already discussed control factors. In fact the population changes in the model are formulated as being controlled by various physical and biological processes varying in space and time, as suggested by the comprehensive school.

4.3 Growth

The simulation model of the growth of one individual mussel as developed by Bayne and Radford (1976), (1981) has been used as a basic tool in the presented population model study.
The model Mytilus of Bayne et al. (1976) integrates the component parts of the energy budget of an individual organism. The increase in dry flesh weight per unit time is equal to the rate of intake of assimilated dry matter minus the sum of the standard and the routine rate of oxygen consumption and the rate of egg production:

$$dW/dt = RIADM - SR - RR - REP$$

where W is the dry flesh weight in mg

RIADM is the rate of intake of assimilated dry matter in mg/day

SR is the standard rate of oxygen consumption converted to an equivalent weight of tissue in mg/day

RR is the routine rate of oxygen consumption converted in the same way to mg/day

REP is the rate of eggs produced or the fecundity in mg dry weight/day

The specification of each of these rates are described by Bayne et al. (1976). Some modifications have been introduced however by the present author and the description of the modified version will be presented here.

Rate of Intake of Assimilated Dry Matter

The filtration rate FR is written as:

$$FR = \frac{1.25 \cdot W^{0.8}}{1 + (\frac{W}{5})^{0.3}} \quad \text{l/day}$$

The rate of filtration is optimum over a very wide range of temperatures normally encountered in natural water. Only at temperatures below say 5°C there is a significant reduction. The temperature reduction function FRT of the filtration rate is written as:

$$\mathrm{FRT} = 0.4 \quad \text{for} \quad T < 2°C$$

$$\mathrm{FRT} = 0.1\ (T-2)+0.4 \quad \text{for}\ 2 < T < 8°C$$

$$\mathrm{FRT} = 1 \quad \text{for} \quad T > 8°C$$

The rate of filtration is specified as not being affected by the concentration of suspended particulates. The amount of dry matter filtered per day is written as:

$$\mathrm{DMFPD} = \mathrm{FA} \cdot \mathrm{FR} \cdot \mathrm{FRT}$$

where FA is the concentration of particulate material at the location of the mussel.

The proportion of filtered material rejected as pseudofaeces is specified in a way which differs from Bayne's formulation. The specification is based on the concept given by Widdows et al. (1979) and depicted in Figure 14.

The difference between the dry matter filtered and the dry matter rejected represents the dry matter ingested DMI.

$$\mathrm{DMI} = \mathrm{DMFPD} \cdot \mathrm{MIN}(1,\ \mathrm{REJCOF}/\mathrm{FA})$$

where, REJCOF is the treshold concentration above which pseudo-faeces production begins, specified as:

$$\mathrm{REJCOF} = 1.36 \cdot W^{0.2}$$

The organic matter intake per day (OMIPD) is obtained by multiplying the dry matter ingested per day with the proportion of organic matter in the dry suspended material PPNOM. So:

$$\mathrm{OMIPD} = \mathrm{PPNOM} \cdot \mathrm{DMFPD} \cdot \mathrm{MIN}(1,\ \mathrm{REJCOF}/\mathrm{FA})$$

The amount of PPNOM is a time dependent forcing function given in Figure 12. A certain proportion of the organic material ingested is assimilated into the body. The assimilation efficiency OAE is written as:

$$OAE = 0.68/(1 + 0.02 \cdot OMIPD)$$

Although the specification differs from the one given by Bayne (1976), the numerical values are quite similar. The intake of assimilated organic matter per day is:

$$RIADM = OAE \cdot OMIPD$$

Observe that the specification of OAE imposes a maximum value on RIADM reached for very large values of the organic matter intake per day which is equal to 0.68/0.02 or 34 mg dry weight per day.

Rates of Oxygen Consumption

The specification of the standard and routine rate of oxygen consumption are according to those given by Bayne et al. (1976).
In the winter the standard rate of oxugen consumption is:

$$SOC = 0.055 \cdot CSATW \cdot W^{0.7} \qquad (ml\ O_2/day)$$

In the summer:

$$SOC = 0.041 \cdot CSATS \cdot W^{0.7} \qquad (ml\ O_2/day)$$

The effects of temperature are incorporated in CSATW and CSATS as given in Table 2.

Table 2 The ratio of oxygen consumption at 15°C and oxygen consumption at T°C

Temperature	Standard rate		Routine rate	
	winter	summer	winter	summer
T	CSATW	CSATS	CRATW	CRATS
---(°C)---				
0	0.617	0.466	0.791	0.575
5	0.689	0.626	0.791	0.668
10	0.803	0.803	0.791	0.953
15	1.000	1.000	1.000	1.000
20	1.284	1.162	1.265	1.048
25	1.708	1.512	1.53	1.45

In the present model version the foregoing winter and summer values are brought together as follows (Radford 1981):

$$SOC = (0.055 \,.\, CSATW \,.\, (1.- SEASIN) + 0.041 \,.\, SEASIN \,.\, CSATS) \,.\, W^{0.7}$$

where SEASIN is defined as a sinusoidal function of time being 1. at the moment of water temperature maximum and 0 at the time the water temperature is lowest.

$$SEASIN = 0.5 \,.\, (1. + \sin \frac{t-125}{365} \,.\, 2\pi)$$

(water temperature is highest at day 216)

where t = time in days reckoned from January 1.

The routine rate of oxygen consumption (ROC) is specified in a similar way. But ROC is also affected by ration level. Bayne and Radford specified these effects of ration in the form of a table listing ROC per unit of metabolic size ($W^{0.7}$) as a function of dry matter filtered per day (Table 3).

$$ROC = (RRATW \,.\, CRATW \,.\, (1. - SEASIN) + RRATS \,.\, CRATS \,.\, SEASIN) \,.\, W^{0.7}$$
($ml\ O_2/day$)

Table 3 The effect of ration on the routine rate of oxygen consumption per unit of metabolic body size

Dry matter filtered per day	Oxygen consumption	
	in winter	in summer
DMFPD	RRATW	RRATS
---($mg.d^{-1}$)---	---($ml\ O_2.d^{-1}\ .\ W^{-0.7}$)---	
0	0	0
2	0.001	0
3	0.015	0.008
5	0.030	0.018
7	0.039	0.025
9	0.048	0.031
11	0.054	0.035
13	0.058	0.038
15	0.060	0.039

The effects of temperature are incorporated in CRATW and CRATS as given in Table 2. The conversion from oxygen to an equivalent dry weight of tissue is 0.96.

So:

$SR = 0.96 \,.\, SOC$ (mg/day)

$RR = 0.96 \,.\, ROC$ (mg/day)

Egg production

In the simulation model an equation for fecundity is used expressed as number of eggs produced during spawning as function of the scope for growth. The data are obtained from Bayne (personal communication). Number of eggs produced (RNEP):

$$RNEP = 3.9 \, . \, 10^{3} \, (1. + GROW/14) \, . \, W$$

where GROW is the scope for growth in mg/day

$$GROW = RIADM - SR - RR$$

Also the egg weight is a function of the scope for growth. The data are again from Bayne (personal communication).
Egg weight:

$$EGW = 80 \, . \, 10^{-6} \, (1. - \exp(- \frac{GROW + 11.1}{5.5})$$

Dry weight loss on spawning is the product of number of eggs produced times egg weight, so:

$$REP = RNEP \, . \, EGW \, \delta(t-te)$$

where $\delta(t-te)$ is the Kronecker delta function, stating that spawning only occurs once a year at time $t = te$. $te = 105 + n.365$, $n = 0,1,2,...$ which is about the middle of April.

5 Model results

5.1 Model results compared to data from an eastern station

According to our food limiting recruitment hypothesis, recruitment should be successful only if FA > FAmin during the period of settlement on the already existing musselbed.

The period of settlement is limited in the model to only one day a year, namely on about 1 August.

Let us take FAmin = 2.5 mg/l.

If the recruitment is successful we still have to describe how successful it will be. Lacking any information on determining factors, we take the simplest assumption namely, recruitment, if successful is a given constant number per square meter. The constant is takes as $5000/m^2$.

The Figures 15, 16, 17 and 18 show the results of a simulation.

The simulation results can be compared to unpublished data obtained by Lambeck at the sampling station Vlije van Bruinisse, in Lake Grevelingen for the years 1973-1978. At the request of Lambeck these unpublished data are not presented here (memo DDMI - 84.591).

We may conclude however that the hypothesis that recruitment is successful only if the food concentration at the time of final settlement is above a given value (FA = 2.5 mg/l), is not falsified by these data from the eastern station Vlije van Bruinisse.

The eastern part of the Grevelingen is more sheltered for wind influence. This fact has two consequences. The first consequence is that the effect of severe storms on the mussels is not detrimental as it is in the western part. The second consequence is that the vertical mixing due to wind generated currents is lower and therefore the vertical food transport to the musselbed will be less. Because the large abundance of the 1972 year class mussels in the eastern station is not reduced during severe storms and the food supply to the musselbed by vertical mixing is not high enough the food concentration appeared too low at the musselbed during July-August to get a successful recruitment. The same arguments were still valid during 1973, 1974 and 1975. During 1976 the abundance of the 1972 year class was reduced enough by natural mortality and predation so that again the food concentration at the musselbed was high enough to quarantee a successful recruitment.

5.2 Model results compared to data from a western station

The western part of the lake is more exposed to wind effects.
The difference with the foregoing situation concerns the effect of severe storms on the zero aged mussels.
According to the weather synopsis of KNMI the most severe storms at the south west coast during the period 1972 up till 1982 occurred on the following days.

Table 1

2 April 1973	day 457
9-11 February 1974	day 771
25 November 1974	day 1059
3 January 1976	day 1463

The hypothesis states that the musselbed on the western part of the lake located at station Archipel, with a depth of only three meters, is severely damaged after such a storm. A mortality factor of 96% for the zero age class mussels during those storms is introduced in the model. So, after each storm only 4% of the newly born recruits are left.

The Figures 19, 20, 21 and 22 show the results of a simulation. A comparison can be made with data obtained by W. Wolff at the sampling station Archipel for the years 1972-1975 (Wolff, Sandee and de Wolf 1977). See Figure 4.
What can be learned from the comparison?
First we observe that the timing in the severe reduction in Figure 22 during the years 1972-1975 coincides with the occurrence of severe storms. The agreement is too good to be accidental. So it is believed that the assumption on the effect of storms on the development of mussels at station Archipel is indeed reliable.
Further we observe from the data that the first successful recruitment after closure occurred in 1972. The closure itself took place May 1971. So, it seems that one complete year is needed to adjust the reproduction cycle of <u>Mytilus edulis</u> to the new tideless situation.
The regular occurring severe storms in the period 1972-1976 maintained a low biomass density at this station. Therefore enough food at the musselbed in

those years was available at the time of settlement to guarantee a successful recruitment.
The last severe storm before 1983 took place January 3, 1976. After 1976 the mussel biomass could grow unmolested, which resulted in a severe competition for food at the musselbed during the critical time of settlement and prevented any further successful recruitment from 1977 onwards. It is to be expected that in the near future the abundance of mussels will be reduced enough by natural causes and perhaps also by the effect of the severe storm of January 1983, to get again a year with successful recruitment, followed by a period of various years without any recruitment and so on.

5.3 Model results compared to new field data

According to the planning, described in working program WABASIM-salt 1985, the draft version of the underlying report, dated October 1983, is completed into the final form in 1985 without testing the model against new field data.
Such a comparison will take place as soon as data become available. The results of this comparison will be reported as an appendix to the final report.

The latest published information over the recruitment success which is available at the moment can be added already to the final version.
The information is based on the report: "Een bestandsopname in voorjaar 1984 van het macrozoobenthos in het Grevelingenmeer", R.H.D. Lambeck and E.B.M. Brummelhuis, DIHO, Rapp. en Verslagen nr. 1985-4.
The authors mention that the mussel biomass seems to have reached its lowest point in spring 1984. The main part of the mussel biomass consists at that time of old mussels probably from 1976 which were in poor condition.

In spring 1982 some young mussel individuals (year class 1981) were present for the first time after years. The survey of 1983 showed again a successful recruitment of restricted magnitude (year class 1982).
The macrozoobenthos survey carried out in April 1984 by the Delta Institute, however, revealed a drastic rejuvenescence of the Mytilus population resulting mainly from a strong 1983 year class.

Observe that the new information on the development of the mussel population given by Lambeck et al. (1985) is not in contradiction with the predictions set down in this report.

6 Conclusions

1. The closure of the Grevelingen estuary in 1971 resulted in a change in water movements from a tidal motion to a wind-driven watercirculation. As a consequence the mussel locations are redistributed because musselbeds are preferable located there where the lateral food transport is maximized, other factors being the same. The lateral flow at the bottom is usually maximal, there were the bottom current is pointing in an uphill direction. The relation between the measured mussel distribution and the calculated wind circulation pattern is shown.

2. The biomass per unit area under steady-state conditions appeared to be more or less proportional to the bottom flow velocity other factors being the same. Because the wind-driven currents in the western part of the lake are stronger than those in the more windsheltered eastern part, the mussel biomass per unit area is greater on the western musselbanks. The mussel biomass density decreases together with the bottom flow velocities at increasing waterdepth.

3. The survival of mussels in shallow areas appeared to be rather limited. It is postulated that this is due to wave action during stormy weather. The slow increase in biomass per square m^2 in the Archipel in the first 5 or 6 years after the closure is ascribed to the high frequency of occurrence of severe storms in that period. Each severe storm in this location nearly eliminated the total stock.

4. The development of the mussel population during the first ten years after closure of the Grevelingen depends to a large extent on the appearance of one or more good brood years. It is shown that the appearance of a good brood year is not correlated with a good year in larvae abundance. We may talk about a good year if the final settlement of larvae is successful. The hypothesis stated in this study, that recruitment is successful only if the food concentration at the musselbed during the period of final settlement (July-August) is higher than a given value (taken as 2.5 mg/l), is not falsified by the available data.

5. The foregoing hypothesis introduces an instability or more exactly speaking a dissimilarity in the year to year pattern of mussel development. Relating recruitment success to food limitation in a closed ecosystem like Lake Grevelingen leads to the following cycle in mussel development:

   a. Recruitment is successful only if the food level in July-August is above a critical value.
   b. The consequence of a successful recruitment is that the food level drops below the critical value in July-August during a number of successive years.
   c. The food level rises, when the population stock on a given bank decreases by mortality until, the cycle starts again with item a.

6. The stability in the development of the mussel population increases, according to the model, under the following environmental conditions:

   a. The magnitude and frequency of occurrence of external impacts, like for instance storms, is increased.
   b. In a closed system like Lake Grevelingen food limitation, if occurring, is more lake wide than in an open tidal system. The latter gradient type situation improves stability, because the chance of a poor year class over the whole area is smaller.
   c. In an open tidal estuary most of the mussel larvae produced each year are "lost" to the North Sea. In such a situation recruitment abundance could possible be limited by larvae abundance. Stability is improved if the density of recruits successful attached each year on a musselbed is not too high.

7. The model results show, that the interval between years with a successful recruitment is shorter in shallow than in deep water.
   This is due to:
   - the greater chance on storm damages in shallow water
   - the low bottom velocity in deep water. A lower food transport rate results in a longer lasting food limiting situation after a successful recruitment year.

8. Interspecific competition between different macrozoobenthos species has not been considered yet.
   The working group WABASIM-salt stresses the importance of this aspect. Especially competition for food and for space between filterfeeders like the mussel and the cockle has to be considered, because it is observed that those species seem to be on the way during the last years to replace the mussel population.
   Further research in this direction is planned for the future.

7 Recommendations for future field research

The question concerning recruitment success appears to be of utmost importance in the development of the mussel population in the Grevelingen Lake. It is recommended to study this problem by placing brood collectors just above existing musselbeds. The numbers of plantigrades settled on these collectors have to be counted on successive observation dates during the period July-August. At the same time the concentration of mussel larvae in the water has to be measured. Also the concentration of particulate organic matter in the neighbourhood of the collectors has to be measured. Because the latter concentration is perhaps too variable it might be more appropriate to take a composite sample over periods of say one or two days. Regular observations on settlement on vertical ropes may also contribute to the solution of this problem.

Finally it is worthwhile to mention that, if the given explanation of the mussel development is indeed true, the future developments can be imrpoved to some extent by thinning out the young mussels on a large scale, especially after a good recruitment year.

The same effect can be expected after the occurrence of a severe storm in winter or spring months. It will be very interesting to monitor whether or not the severe storm, which occurred at the beginning of this year (1983), would have had a beneficial effect on the recruitment of mussels in the second half of 1983.

LITERATURE

BATCHELOR, G.K.
An introduction to Fluid Dynamics
Cambridge University Press, Cambridge, 1967

BAYNE, B.L. (editor)
Marine Mussels: Their Ecology and Physiology
Int. Biological Programme 10
Cambridge University Press, Cambridge, 1976

BAYNE, B.L. and C.M. WORRAL
Growth and Production of Mussels Mytilus edulis from Two Populations
Marine Ecology Progr. Ser. Vol. 3, pp. 317-328, 1980

BAYNE, B.L. (to be published)
The physiological Ecology of Marine Molluscan Larvae
Chapter 8 in: The Biology of Molluscs: Reproduction and Development
Editors: N.H. Verdonk, A. Tourpa and J.A.M. van den Biggelaar
Academic Press, London, New York

BEVERTON, R.J.H. and S.J. HOLT
On the Dynamics of Exploited Fish Populations
Fishery Investigations, Ser. II, Vol. 19, 533 pp., 1957

DARE, P.J.
The Settlement, Growth and Survival of Mussels Mytilus edulis L. in Morecambe Bay, England
International Council for the Exploration of the Sea, CM 1969/K: 18, pp. 1-8 (Mimeo.), 1969

DARE, P.J.
Preliminary Studies on the Utilization of the Resources of Spat Mussels, Mytilus edulis L. occurring in Morecambe Bay, England
International Council for the Exploration of the Sea, CM 1971/K: 11, pp. 1-6 (Mimeo.), 1971

LITERATURE (continuation)

DARE, P.J.
Settlement, Growth and Production of the Mussel Mytilus edulis L. in Morecambe Bay
Fishery Investigations. Ministery of Agriculture, Fisheries and Food, London, Series II, 1975

GRIFFITHS, R.J.
Population Dynamics and Growth of the Bivalve Choromytilus meridionalis (Kr.) at Different Tidal Levels
Estuarine, Coastal and Shelf Science, Vol. 12, pp. 101-118, 1981

HANCOCK, D.A.
The Relationship between Stock and Recruitment in Exploited Invertebrates
Rapport et Procesverbaux des Reunions. Conseil Permanent International pour l'Exploration de la Mer, 164, pp. 113-131, 1973

KAUTSKY, N.
Growth and Size Structure in a Balthic Mytilus edulis Population
Marine Biology, Vol. 68, pp. 117-133, 1982

KAUTSKY, N.
Quantitative Studies on Gonad Cycle, Fecundity, Reproductive Output and Recruitment in a Baltic Mytilus edulis Population
Marine Biology, Vol. 68, pp. 143-160, 1982

LAMBECK, R.H.D.
Effects of Closure of the Grevelingen Estuary on Survival and Development of Macrozoobenthos
In "Feeding and Survival Strategies of Estuarine Organisms" edited by Jones, N.V. and W.J. Wolff, W.J.
Plenum Publ. Corp. pp. 153-158, 1981

LITERATURE (continuation)

LAMBECK, R.H.D.
Colonization and Distribution of Nassarius Reticulatus (Mollusca: Prosobranchia) in the Newly Created Saline Lake Grevelingen (SW Netherlands)
Netherlands Journal of Sea Research, Vol. 16, pp. 67-79, 1982

LAMBECK, R.H.D.
Productivity of Mytilus edulis in Saline Lake Grevelingen
Netherlands Journal of Sea Research (In preparation)

LINDIJER, G.J.H.
Three-dimensional Circulation Models for Shallow Lakes and Seas
Delft Hydraulics Laboratory, Report R 900-III (in Dutch), 1981

MAAS GEESTERANUS, R.A.
On the Formation of Banks by Mytilus edulis
Archives Neerlandaises Zoologie, 6, pp. 283-325, 1942

MAY, R.M.
Theoretical Ecology. Principles and Applications
Blackwell Scientific Publications, Oxford, 1976

RADFORD, P.J., I.R. JOINT and A.R. HILBY
Simulation Models of Individual Production Processes
In "Analysis of Marine Ecosystems" edited by A.R. Longhurst
Academic Press, London, New York, pp. 677-701, 1981

SCHOOT, E. v.d.
The Contribution of Asterias rubens in the Carbon Cycle of Lake Grevelingen (in Dutch)
Doct. Report-D5, Delta Institute for Hydrobiological Research, the Netherlands, 1974

LITERATURE (continuation)

THORSON, G.
Some Factors Influencing the Recruitment and Establishment of Marine Benthic Communities
Netherlands Journal of Sea Research, Vol. 3, pp. 267-293, 1966

VERHAGEN, J.H.G.
A Distribution and Population Model of the Mussel Mytilus edulis in Lake Grevelingen
In "Analysis of Ecological Systems: State-of-the-Art in Ecological Modelling"
Editors: Lauenroth, W.K., Skogerboe G.V. and Flug M., pp. 373-383, 1983

VERWEY, J.
On the Ecology of Distribution of Cockle and Mussel in the Dutch Waddensea. Their Role in Sedimentation and the Source of their Food Supply
Archives Neerlandaises de Zoologie, Tome 10, 1951-1954, 2e Livre, pp. 171-240, 1952

WIDDOWS, J., P. FIETH and C.M. WORRALL
Relationships between Seston, Available Food and Feeding Activity in the Common Mussel Mytilus edulis
Marine Biology 50, pp. 195-207, 1979

WILDISH, D.J. and D.D. KRISTMANSON
Tidal Energy and Sublittoral Macrobenthic Animals in Estuaries
Journ. Fish. Res. Board Can., Vol. 36, pp. 1197-1206, 1979

WINTER, J.E.
A Review of the Knowledge of Suspension Feeding in Lamellibranchiate Bivalves with Special Reference to Artificial Aquaculture Systems
Aquaculture, 13, pp. 1-33, 1978

LITERATURE (continuation)

WOLFF, W.J.
A Benthic Food Budget for the Grevelingen Estuary, the Netherlands, and a Consideration of the Mechanisms Causing High Benthic Secondary Production in Estuaries Ecology of Marine Benthos
Editor: Coull, B.C. Univ. of South Carolina Press., pp. 267-280, 1977

WOLFF, W.J., F. VEGTER, H.G. MULDER and T. MEIJS
The Production of Benthic Animals in Relation to the Phytoplankton Production. Observations in the Saline Lake Grevelingen, the Netherlands
10th Europ. Symp. on Marine Biology, Ostend, Belgium, Vol. 2, pp. 653-672, 1975

WOLFF, W.J., A.J.J. SANDEE and L. de WOLF
The Development of a Benthic Ecosystem
Hydrobiologia, Vol. 52, I, pp. 107-115, 1977

WOLFF, W.J. and L. de WOLF
Biomass and Production of Zoobenthos in the Grevelingen Estuary
The Netherlands Estuarine and Coastal Marine Science, Vol. 5, pp. 1-24, 1977

ZISON, S.W., W.B. MILLS, D. DEIMER and C.W. CHEN
Rates, constants and kinetics formulations in surface water quality modelling
EPA-600/3-78-105, Athens, Georgia, 1978

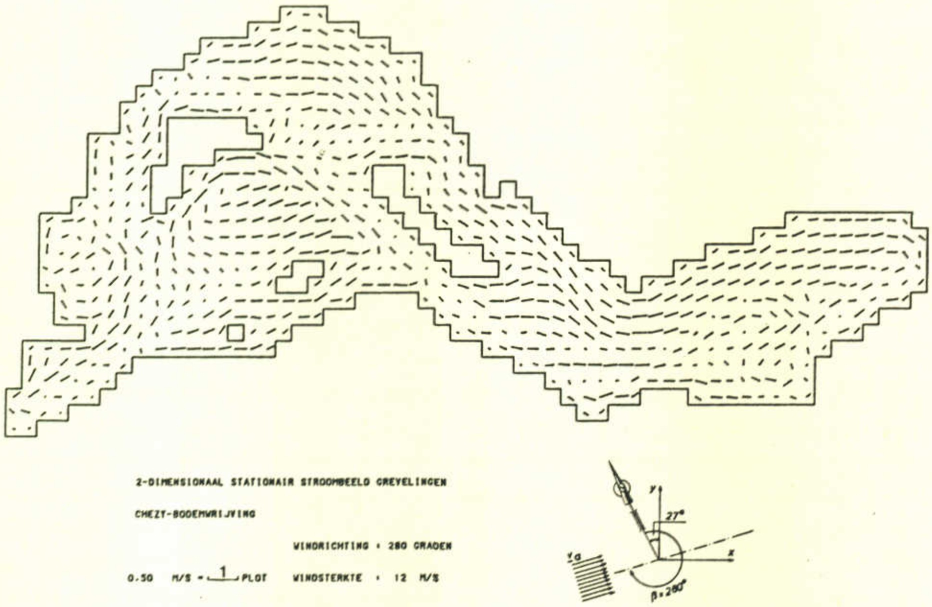


Figure 1. Calculated circulation pattern of vertical averaged flow in Lake Grevelingen

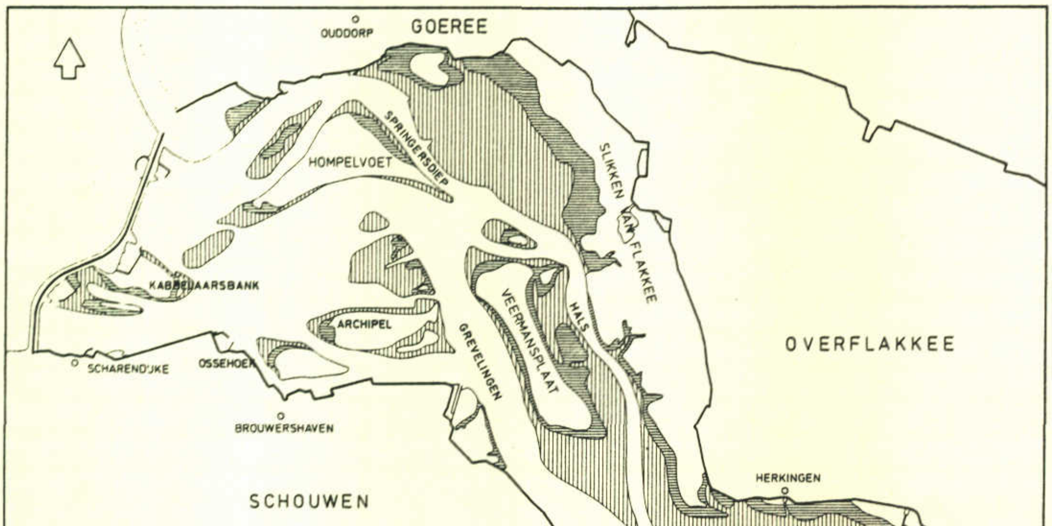


Figure 2. Map of shallows and gullies in Lake Grevelingen

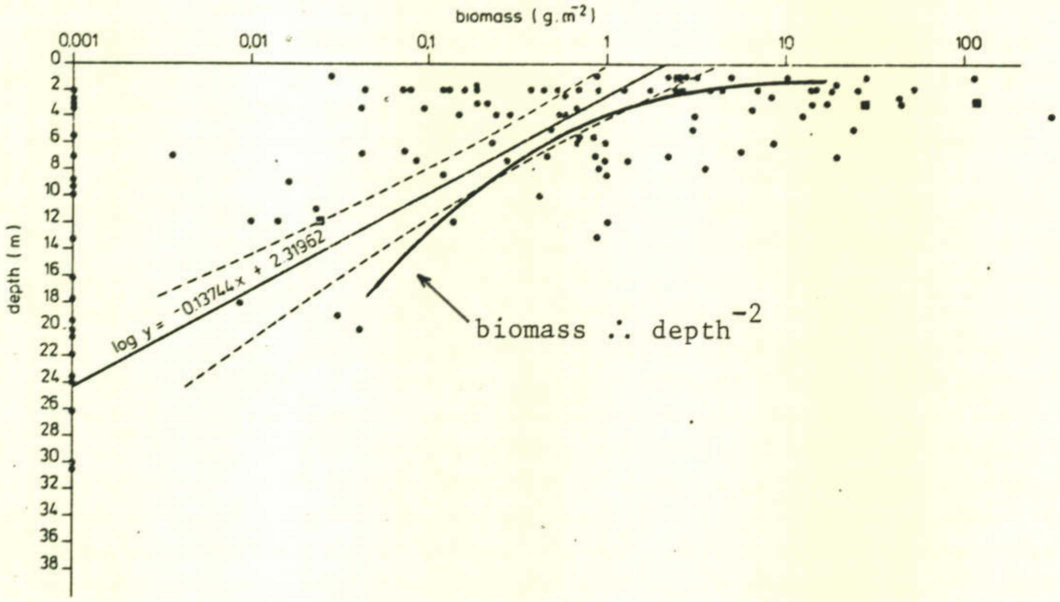


Figure 3. Relationship between depth and benthic biomass (95% confidence limits) in Lake Grevelingen in April 1973. (Wolff et al. 1975)

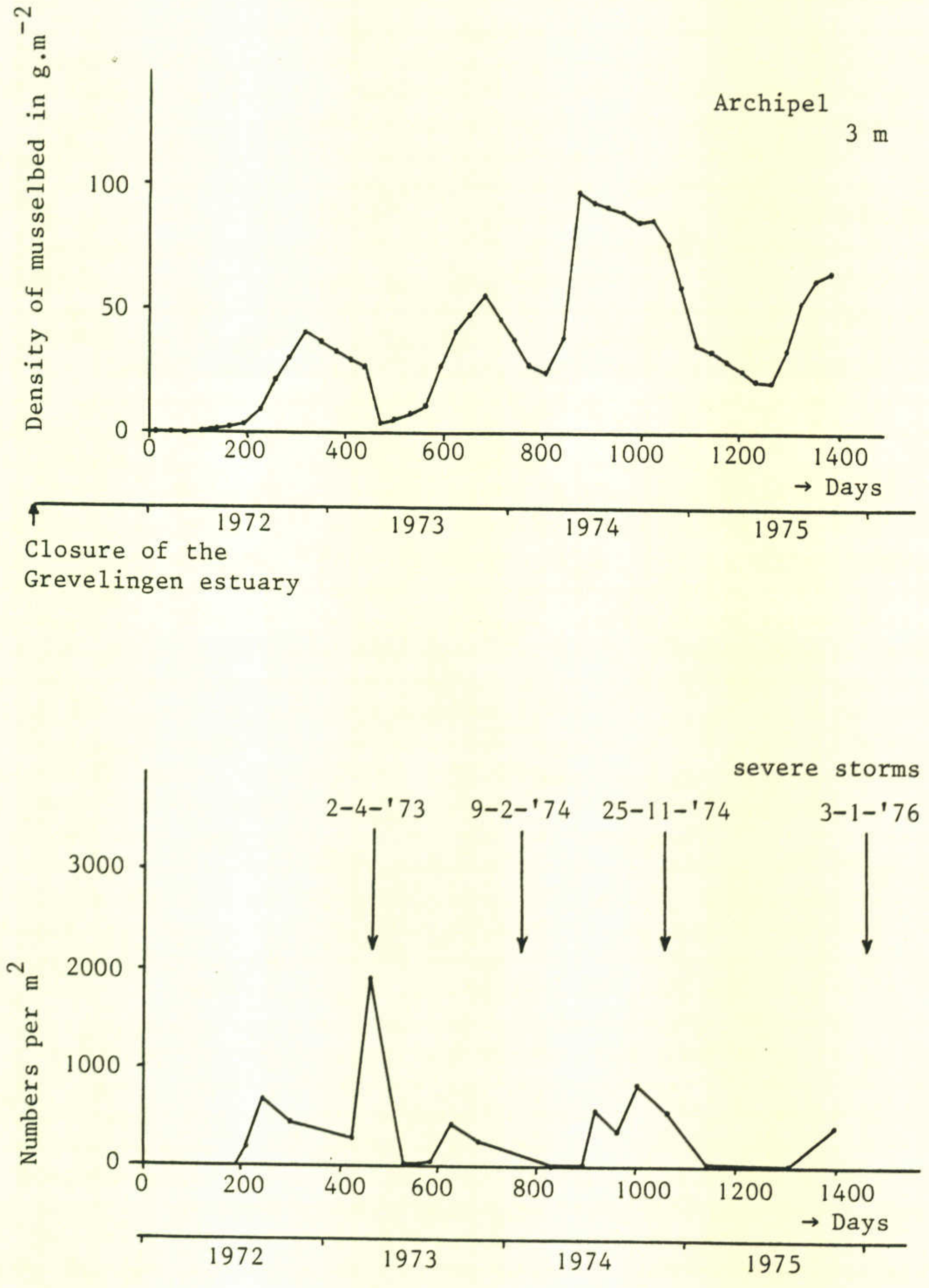


Figure 4. The development of the population in weight and numbers per m^2 as measured

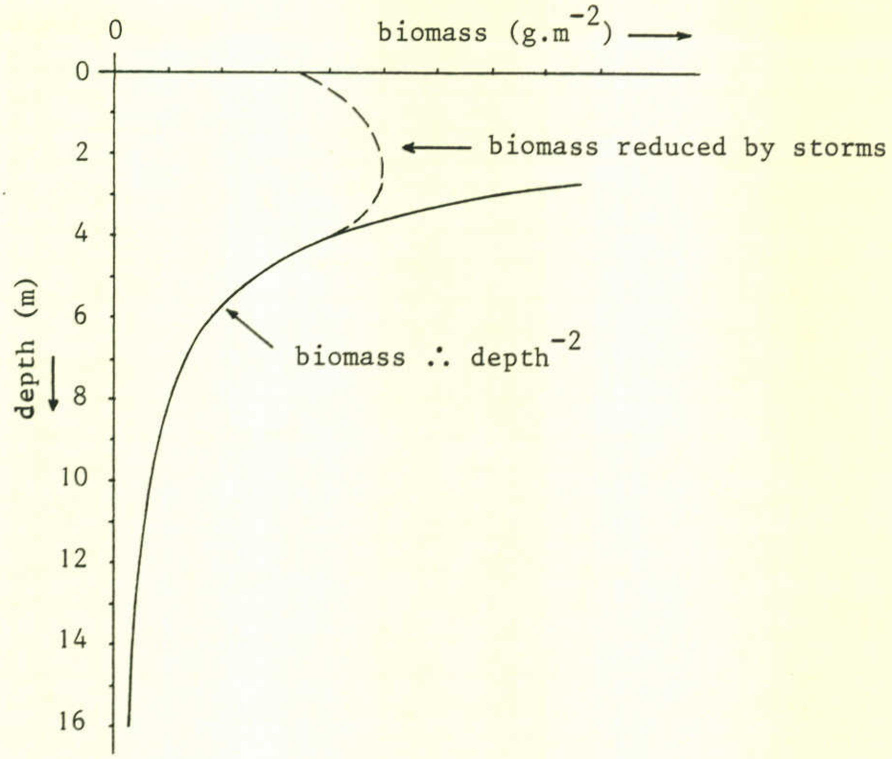


Figure 5. Theoretical relationship between depth and benthic biomass in Lake Grevelingen

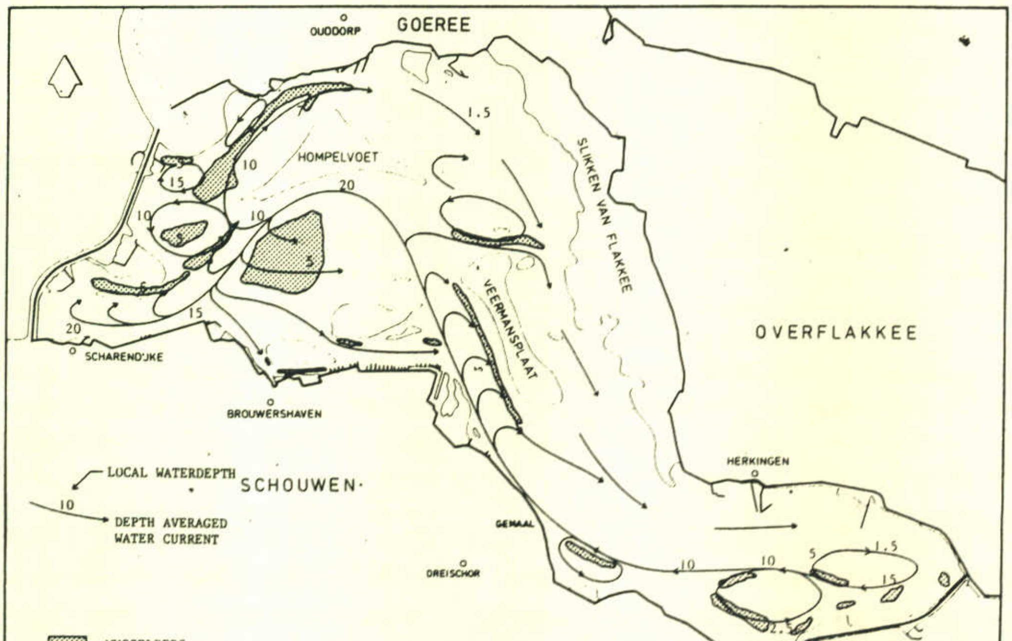


Figure 6. Distribution of musselbeds in Lake Grevelingen and the wind driven circulation pattern

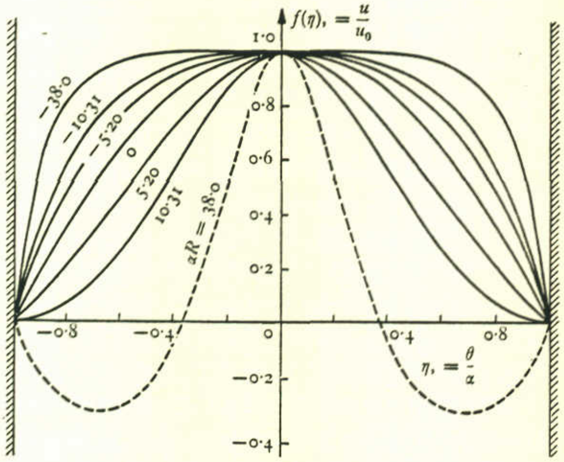


Figure 7. Symmetrical distributions of radial velocity in a divergent channel for various values of αR ($= \alpha^2 r u_o / v$). Positive values of αR represent outflow at the centre of the channel (Batchelor, 1967)

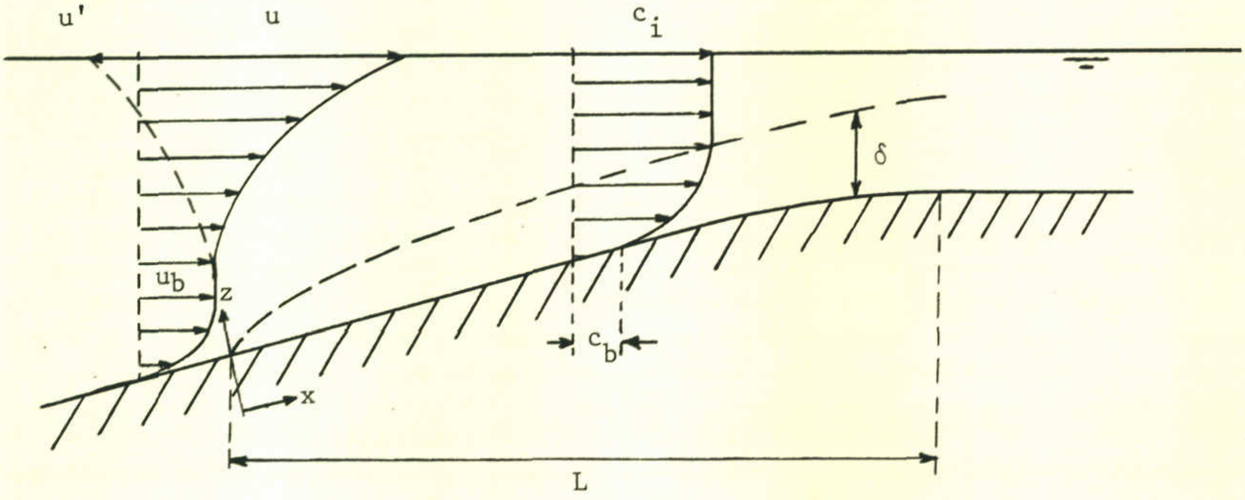


Figure 8. A musselbed on a sloping bottom in a wind-driven convergent flow

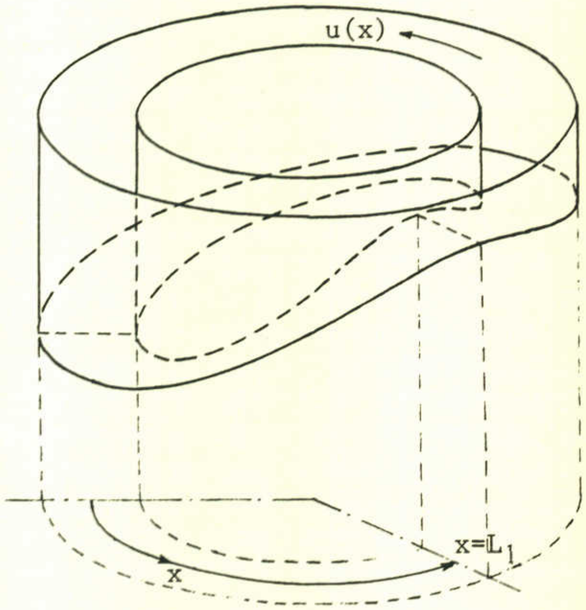


Figure 9. Mussels partly covering the bottom of this circular channel consume the algae growing in the steady water flow

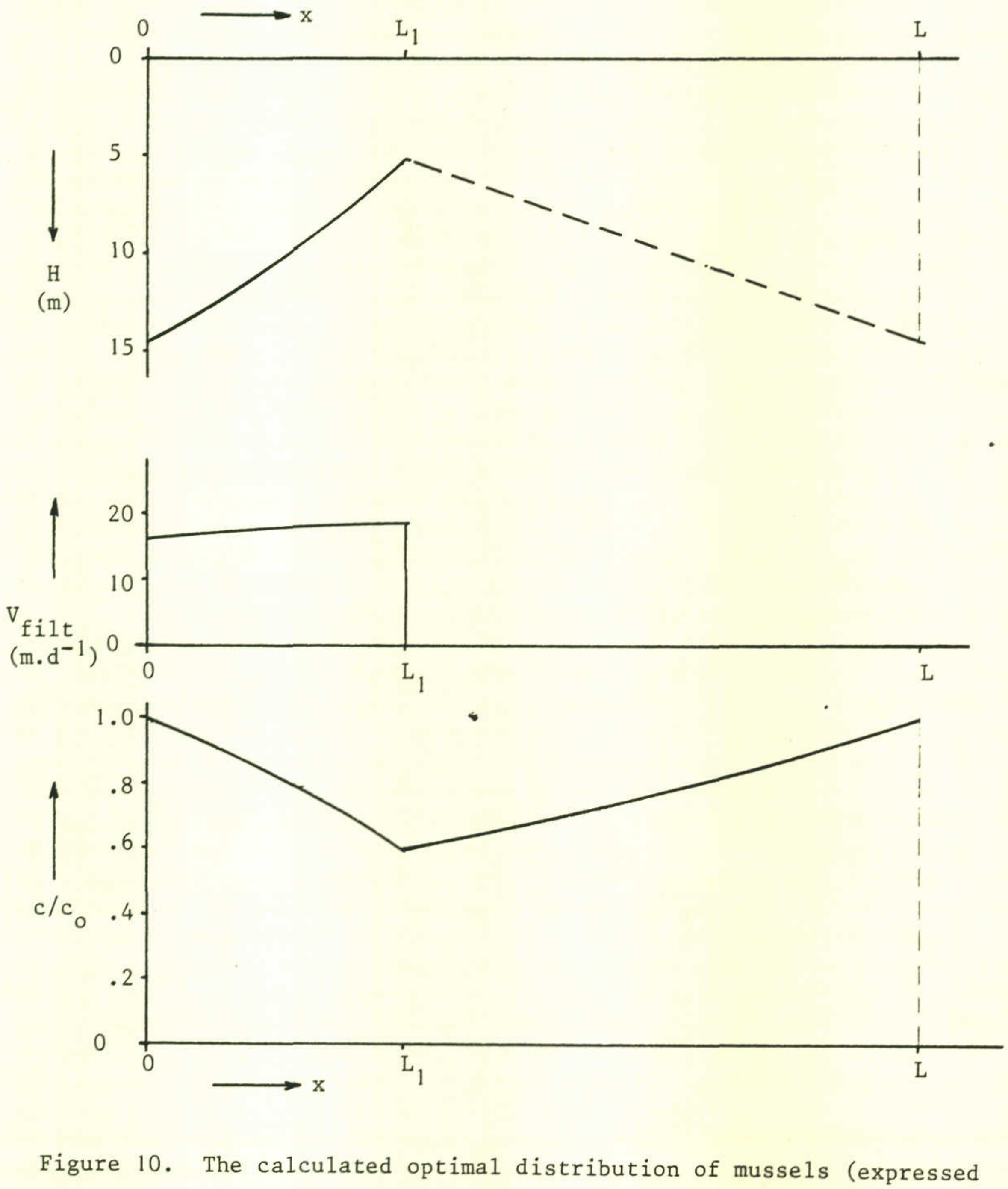


Figure 10. The calculated optimal distribution of mussels (expressed in V_{filt}) and the resulting algae concentration distr. c/c_o in the circular channel with a depth distr. as given

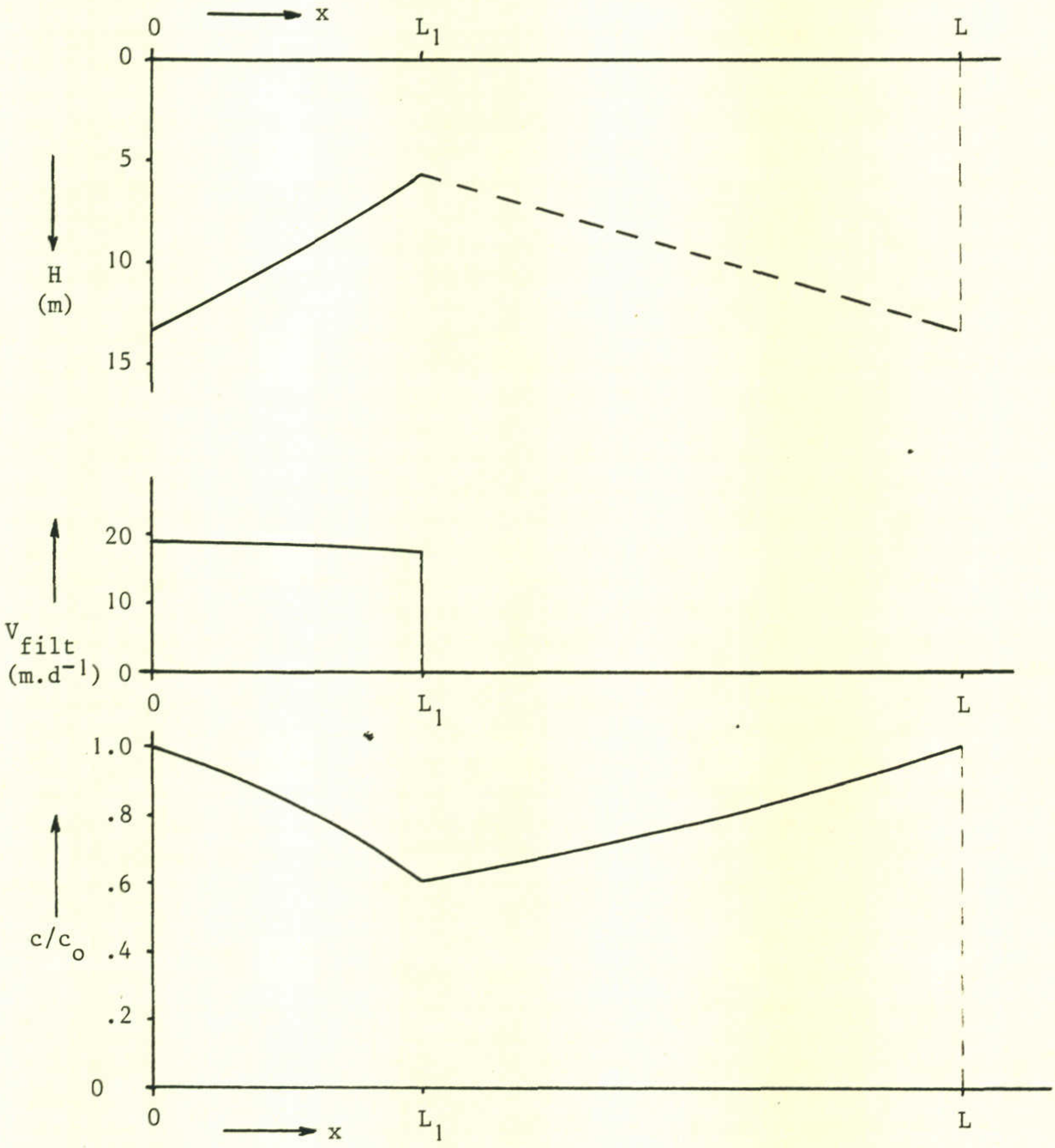


Figure 11. The calculated optimal distribution of mussels (expressed in V_{filt}) and the resulting algae concentration distr. c/c_o in the circular channel with a depth distr. as given

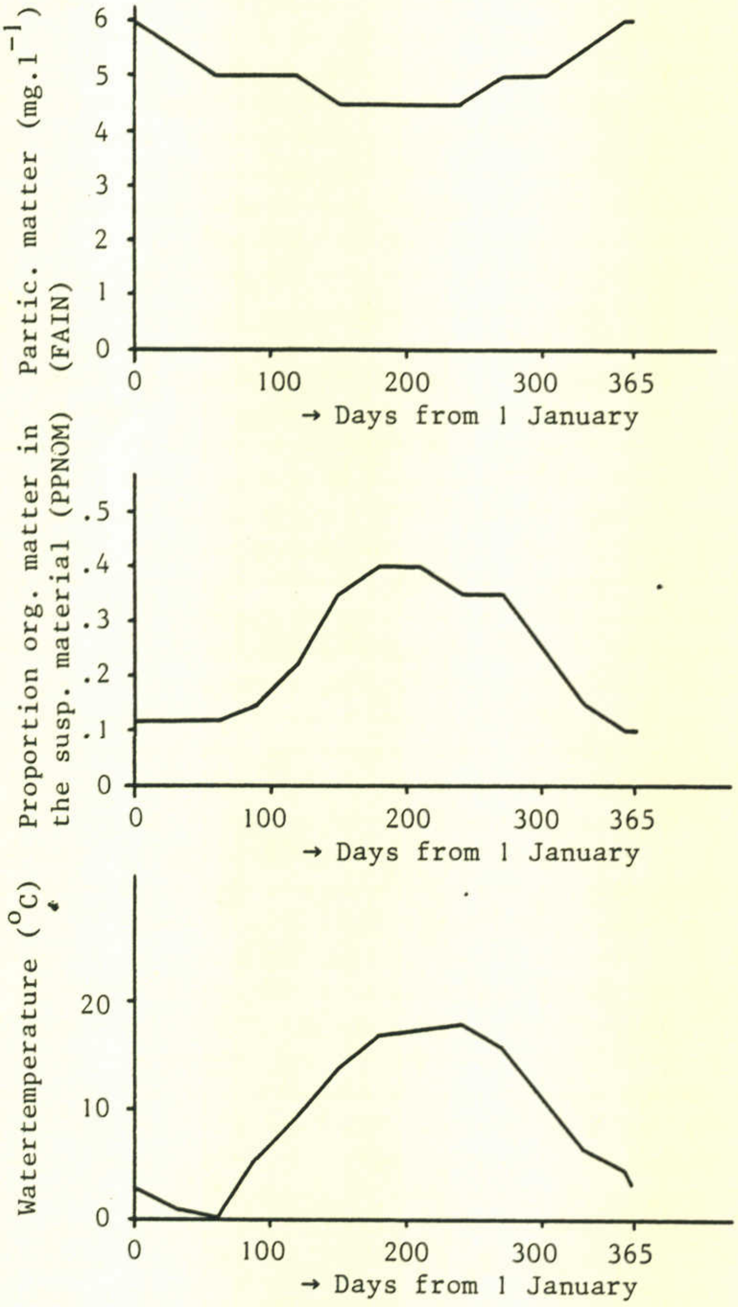


Fig. 12. The annual cycle in particulate material, the proportion of organic matter in the particulate material and the water temperature in the inlet water of the reservoir

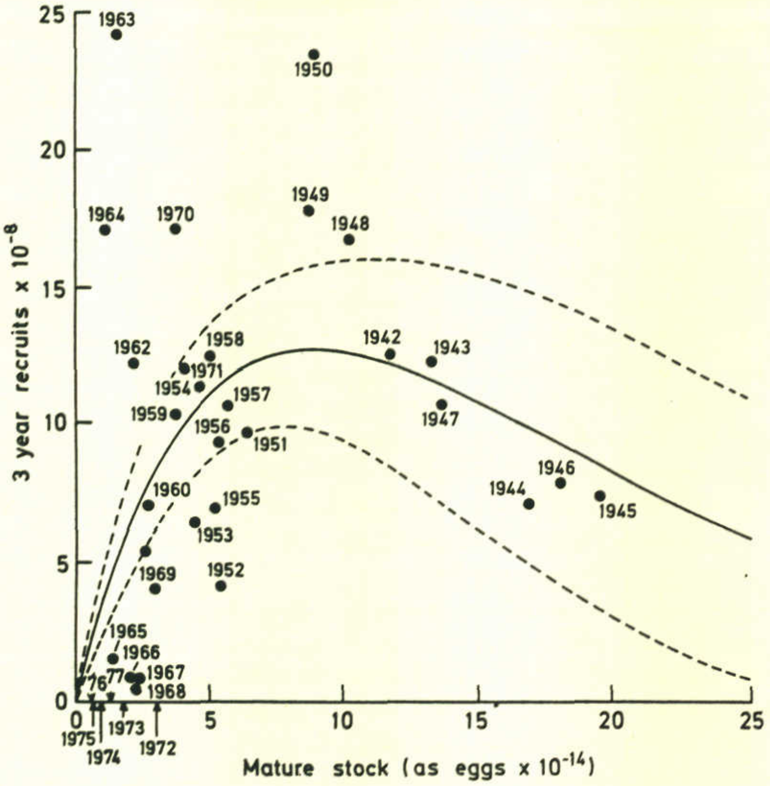


Figure 13. The dependence of recruitment, in numbers, on stock (as eggs) in the Arcto-Norwegian cod population (Garrod and Jones, 1974); the dotted lines show the error curves of the least-square fit, i.e. there is one chance in 20 that the true curve lies outside the error lines

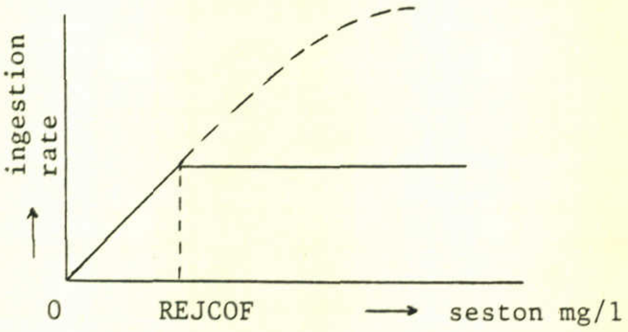


Figure 14. Ingestion rate as a function of particle concentration

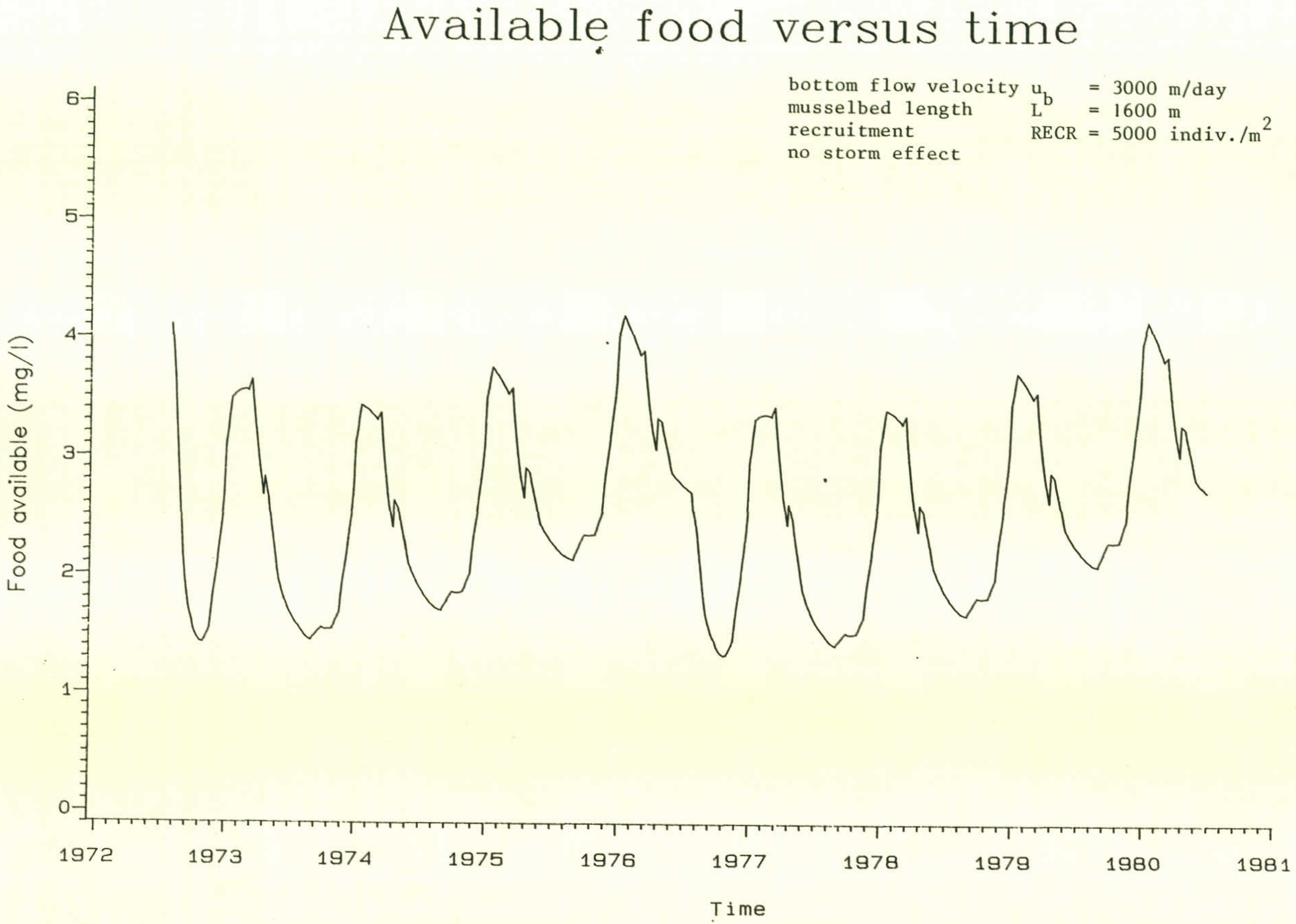

Available food versus time
bottom flow velocity u_b = 3000 m/day
musselbed length L^b = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Food available (mg/l)
0
1
2
3
4
5
6
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 15

Biomass density versus time

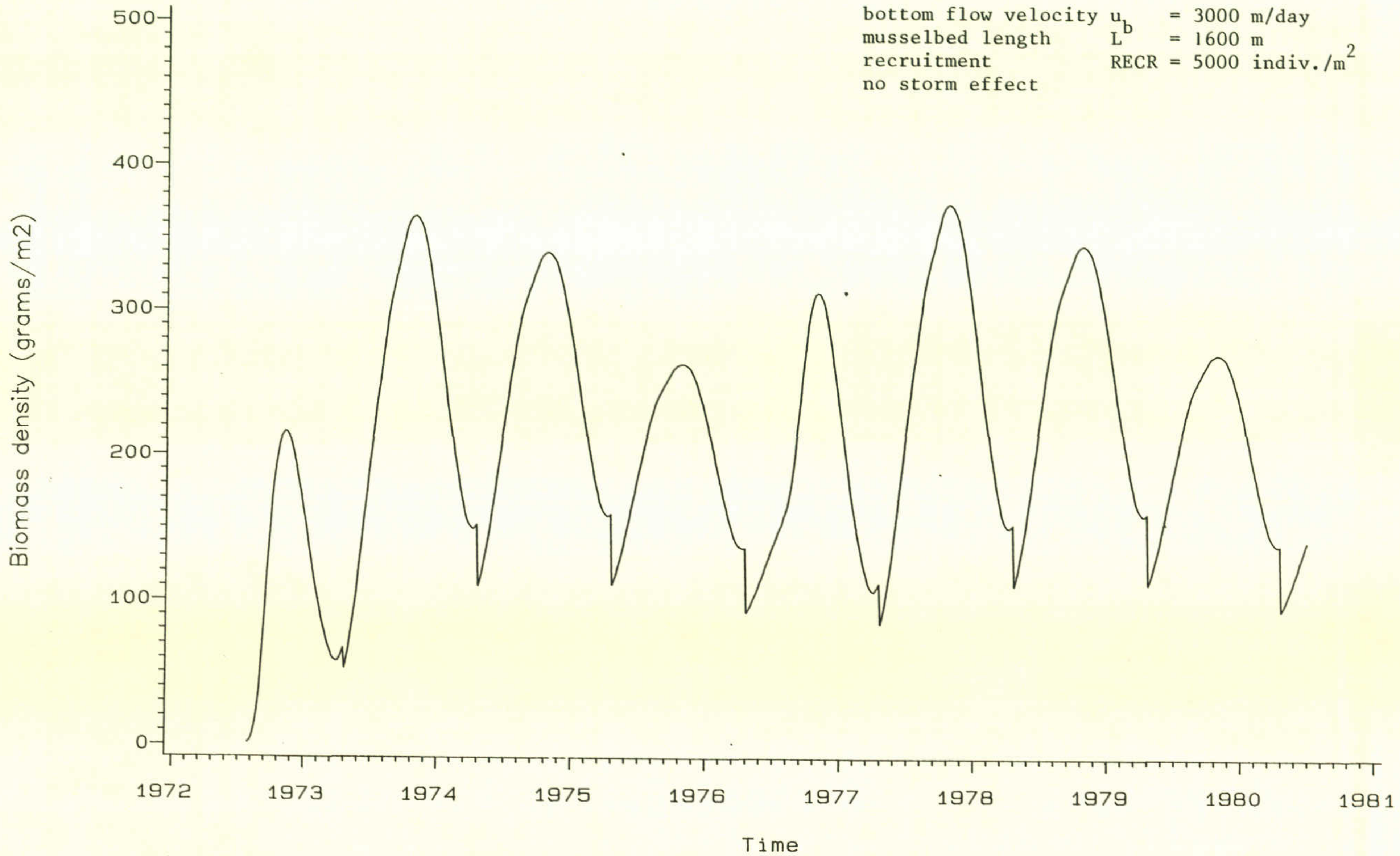


Figure 16

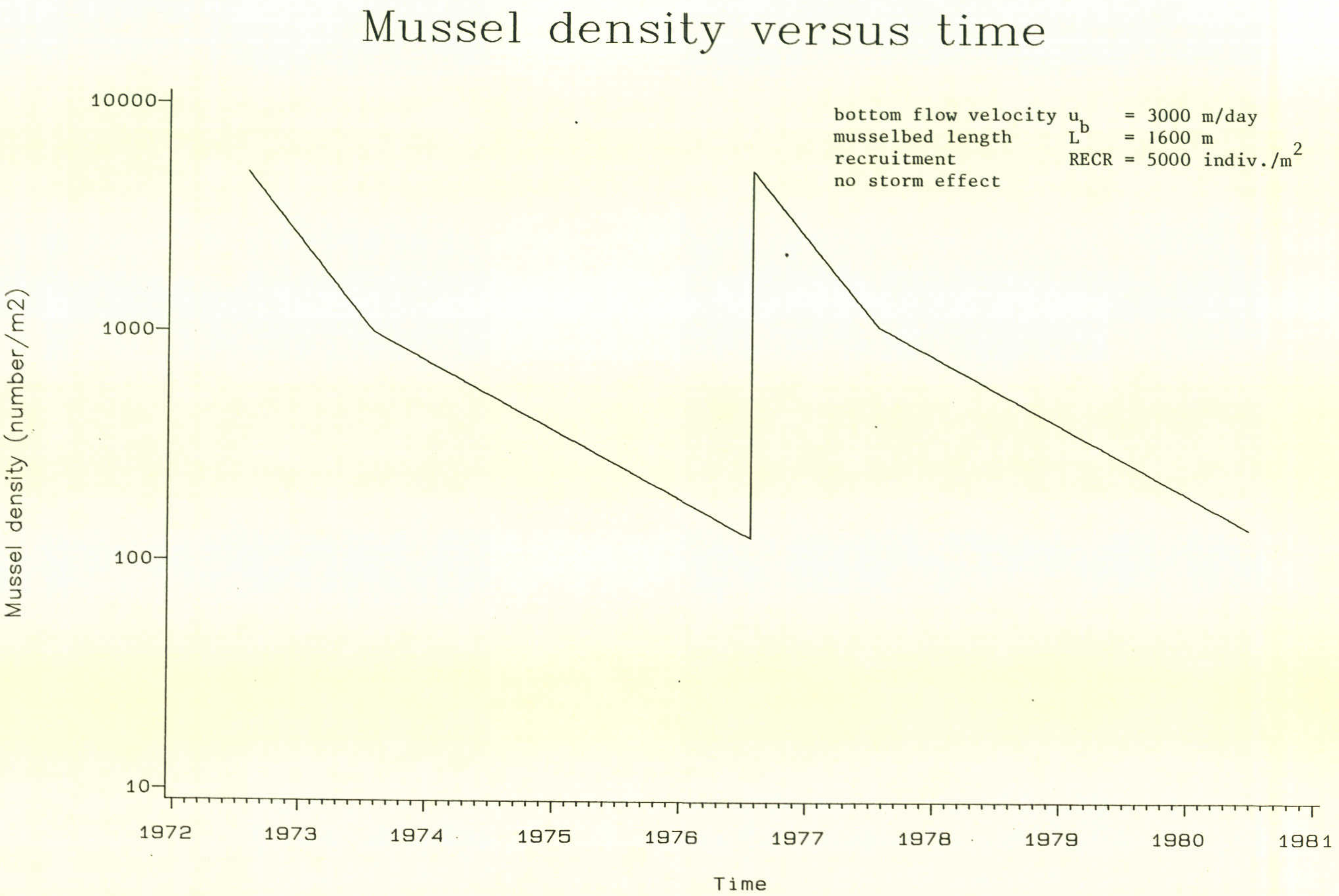

Mussel density versus time
bottom flow velocity u_b = 3000 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Mussel density (number/m2)
10000
1000
100
10
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 17

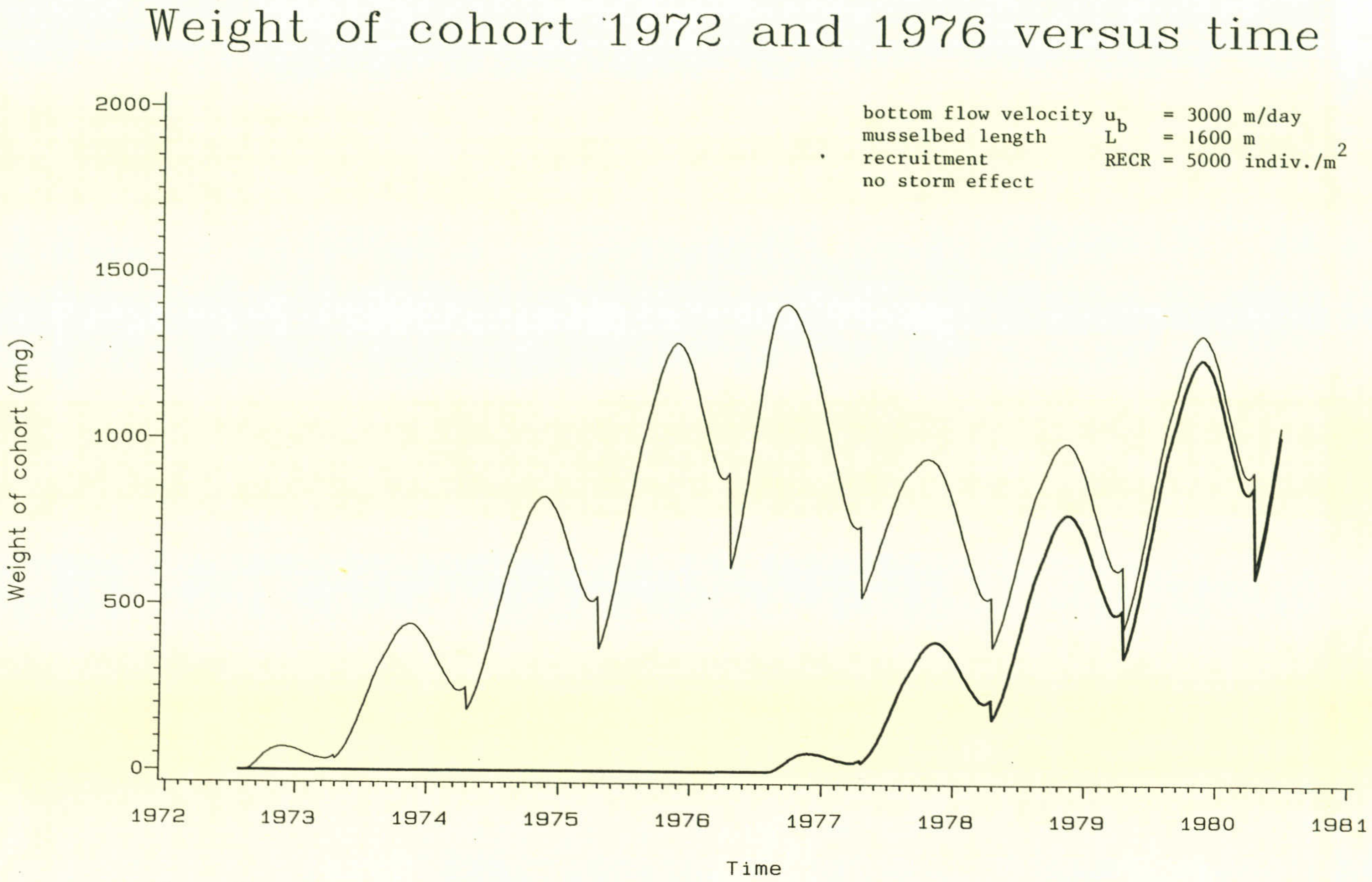

Weight of cohort 1972 and 1976 versus time
bottom flow velocity u_b = 3000 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Weight of cohort (mg)
2000
1500
1000
500
0
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 18

Available food versus time

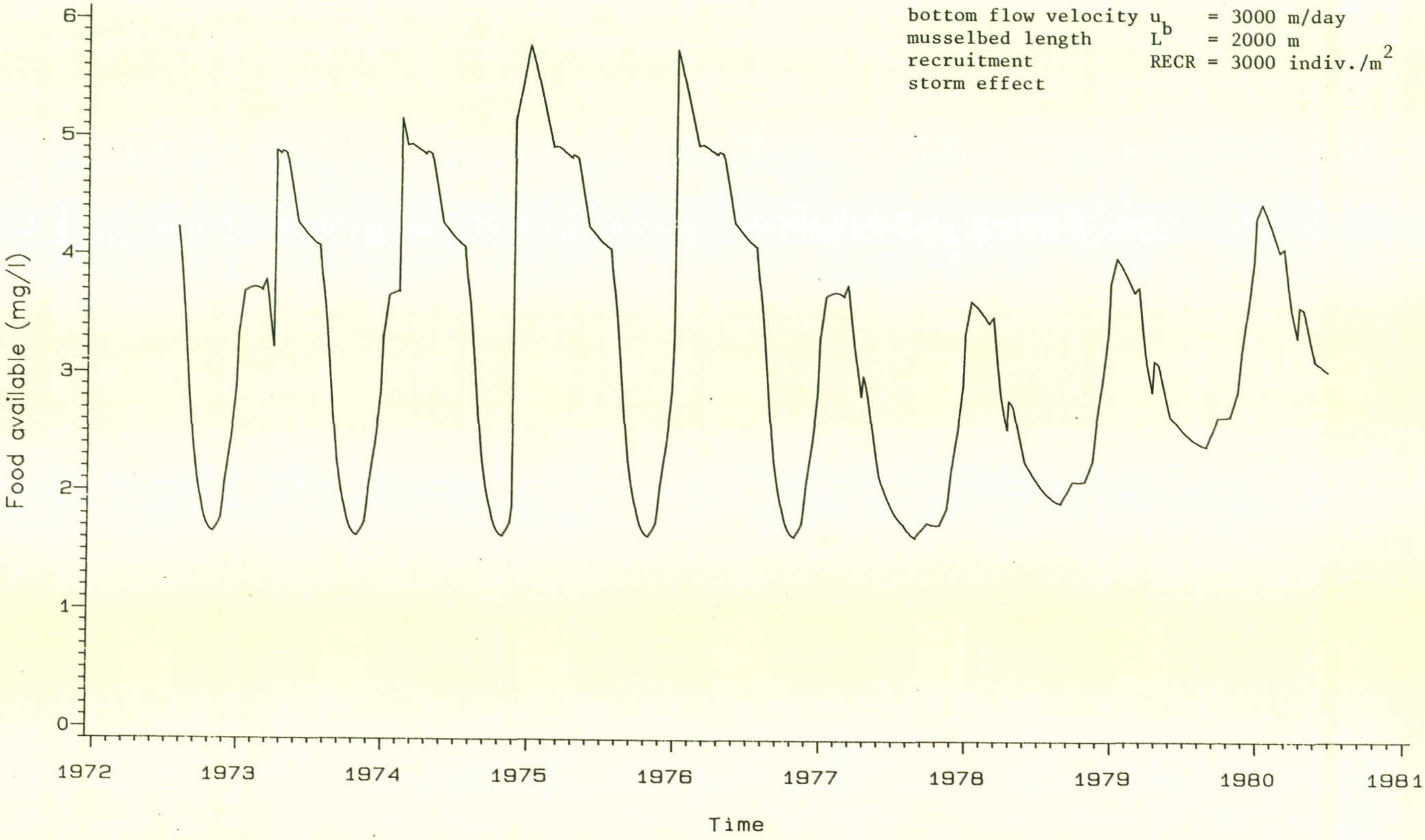


Figure 19

Biomass density versus time

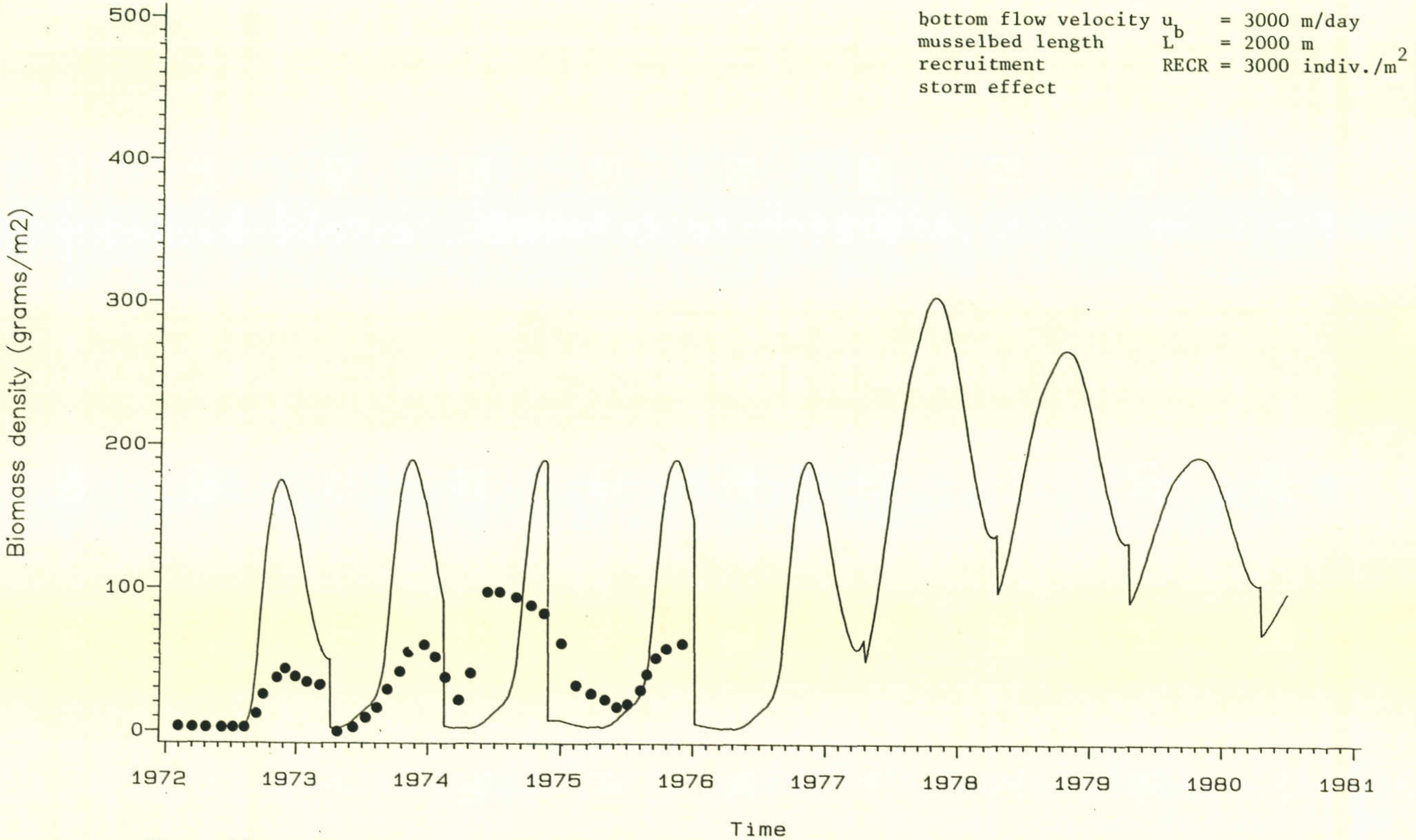


Figure 20

data Wolff et al. 1977

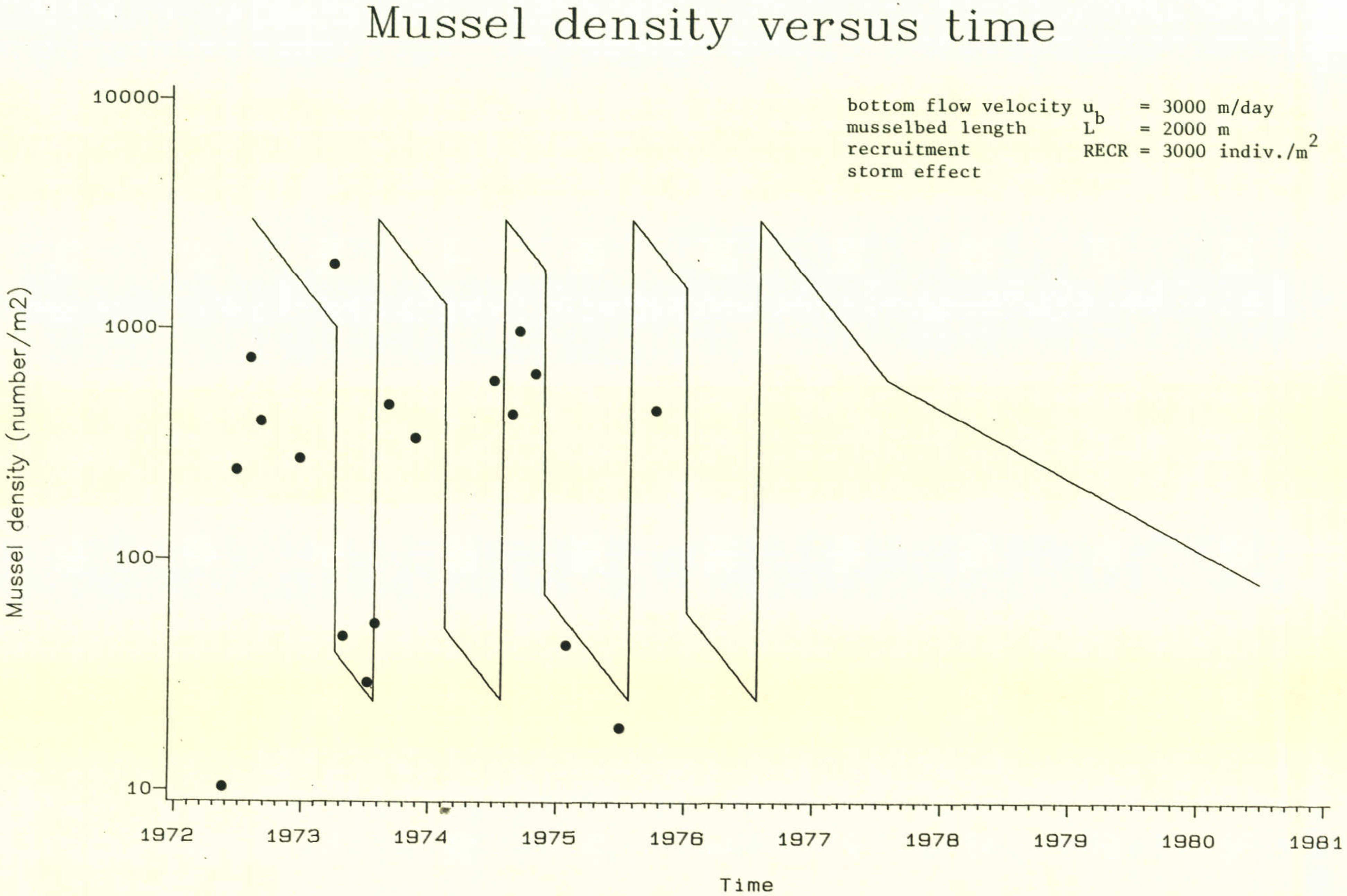


Figure 21

data Wolff et al. 1977

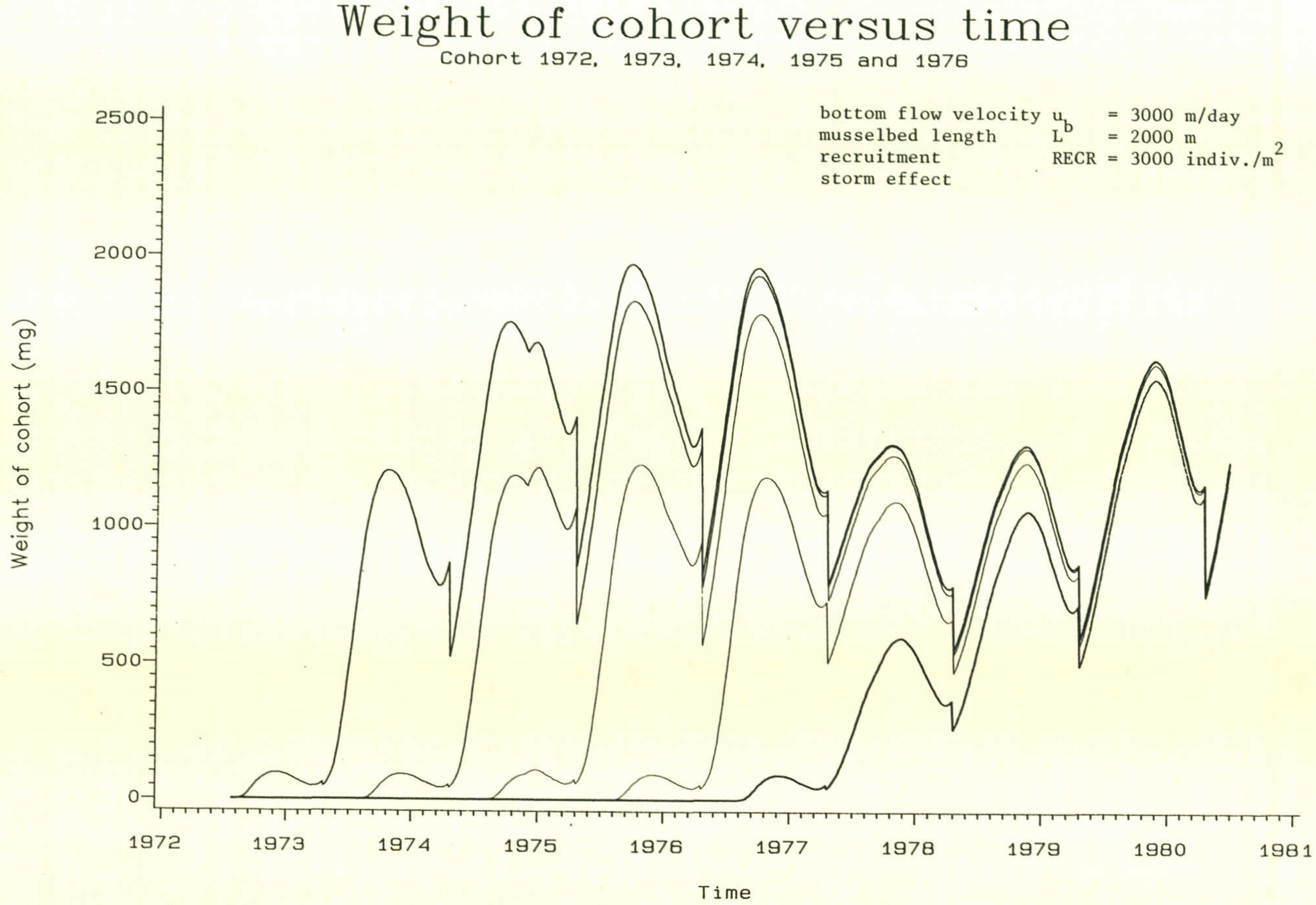

Weight of cohort versus time
Cohort 1972, 1973, 1974, 1975 and 1976
bottom flow velocity u_b = 3000 m/day
musselbed length L = 2000 m
recruitment RECR = 3000 indiv./m^2
storm effect
Weight of cohort (mg)
2500
2000
1500
1000
500
0
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 22

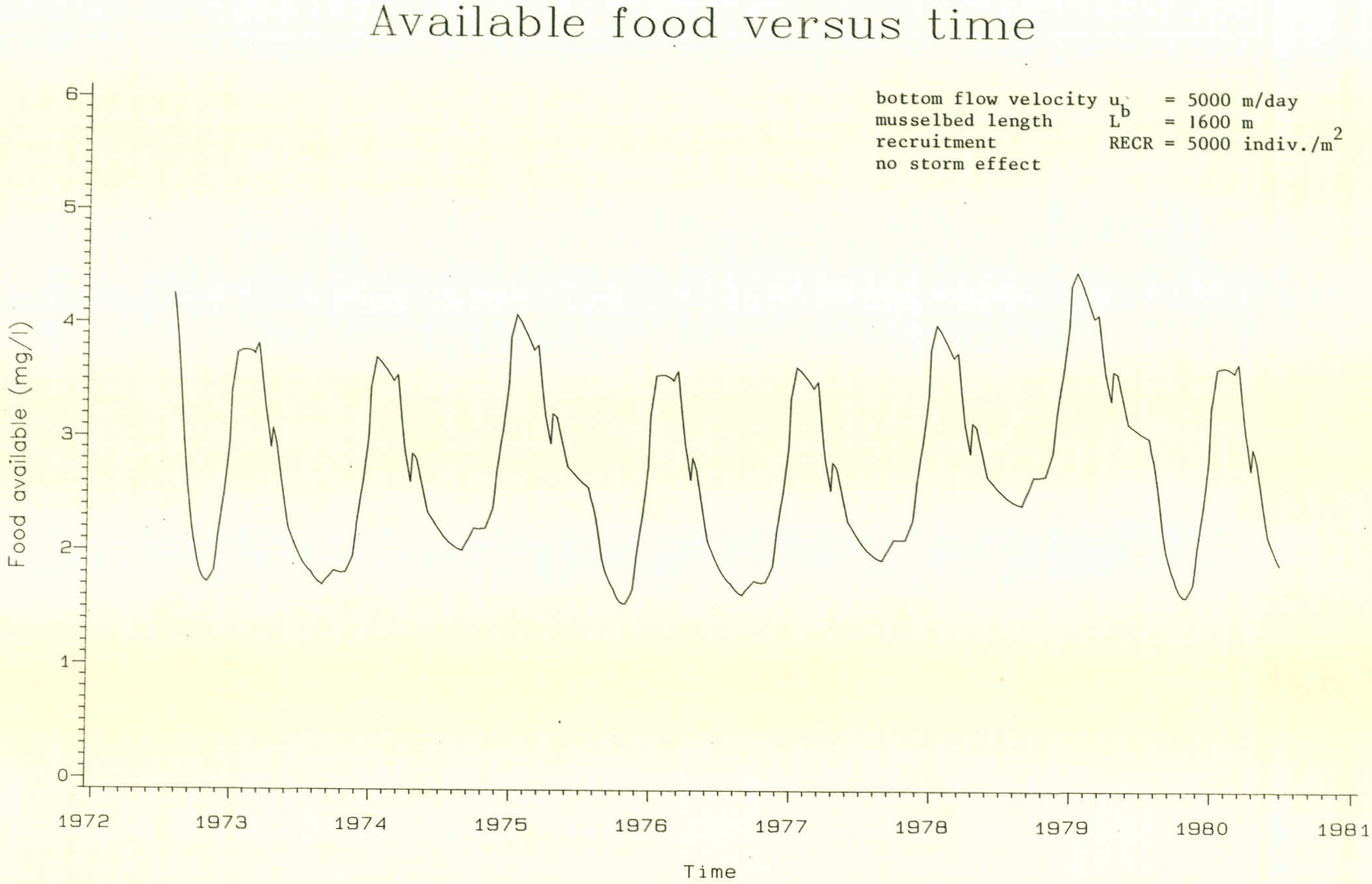

Available food versus time

Figure 23

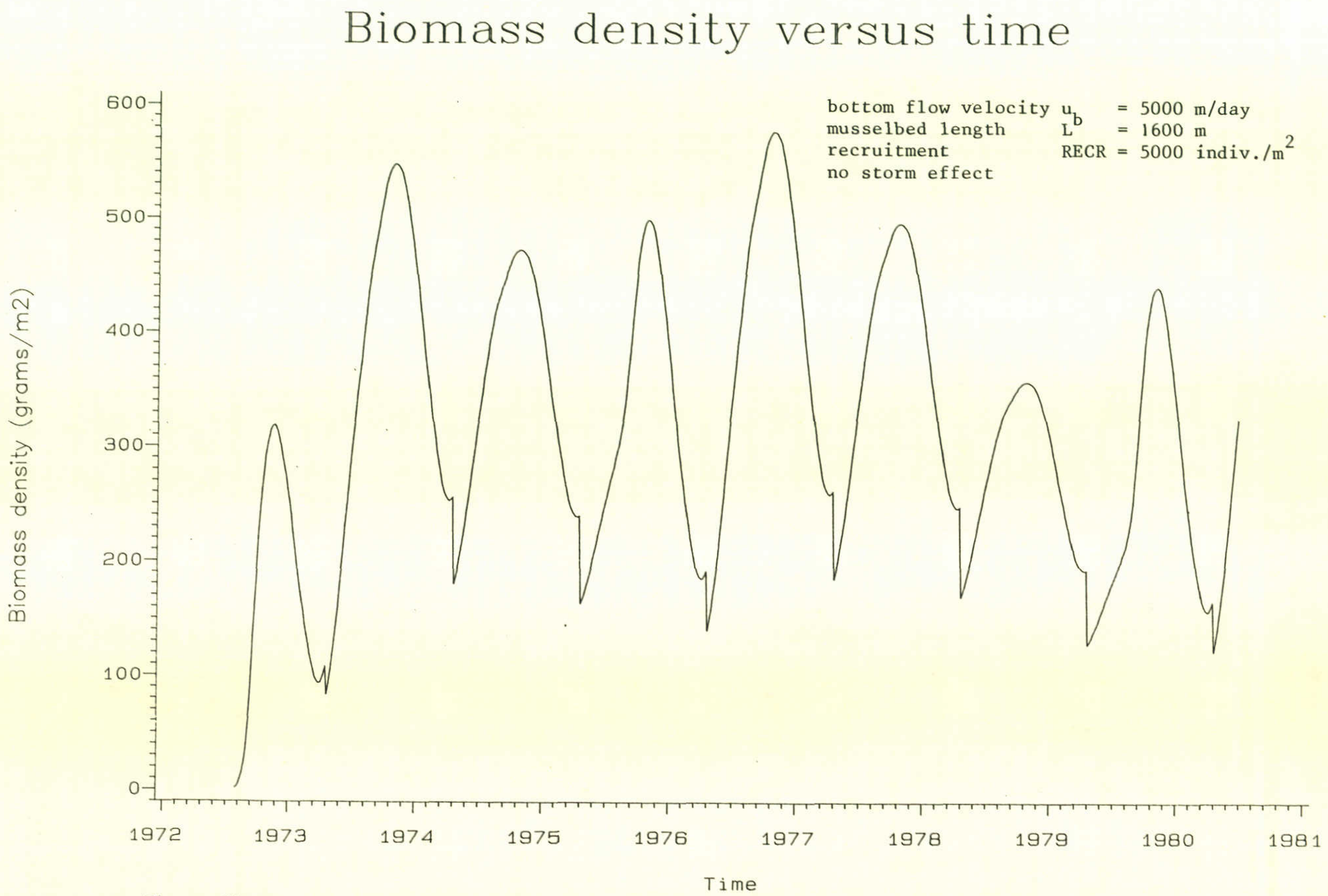

Biomass density versus time

Figure 24

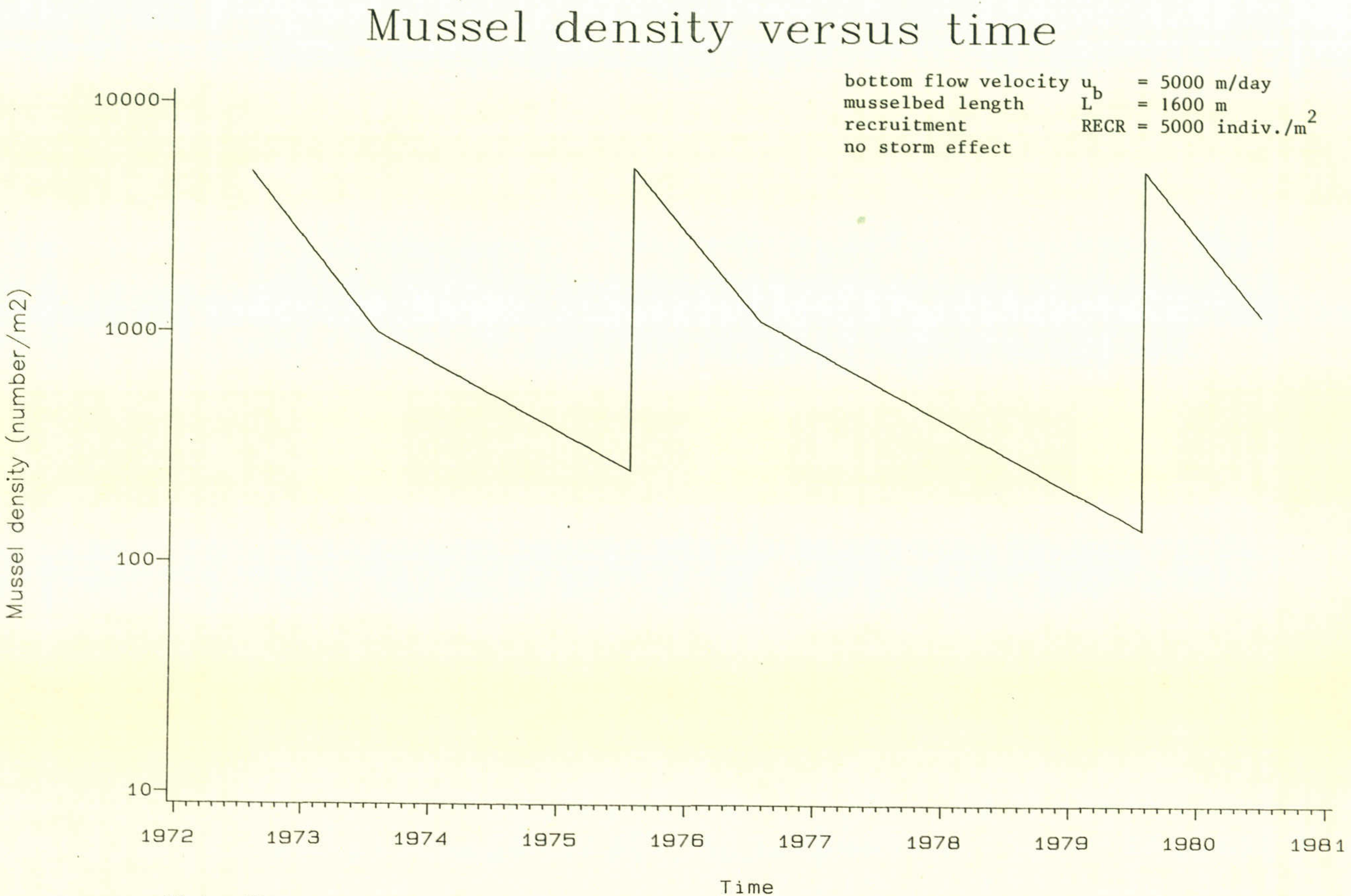

Mussel density versus time
bottom flow velocity u_b = 5000 m/day
musselbed length L^b = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Mussel density (number/m2)
10000
1000
100
10
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 25

Weight of cohort 1972, 1975 and 1979 versus time

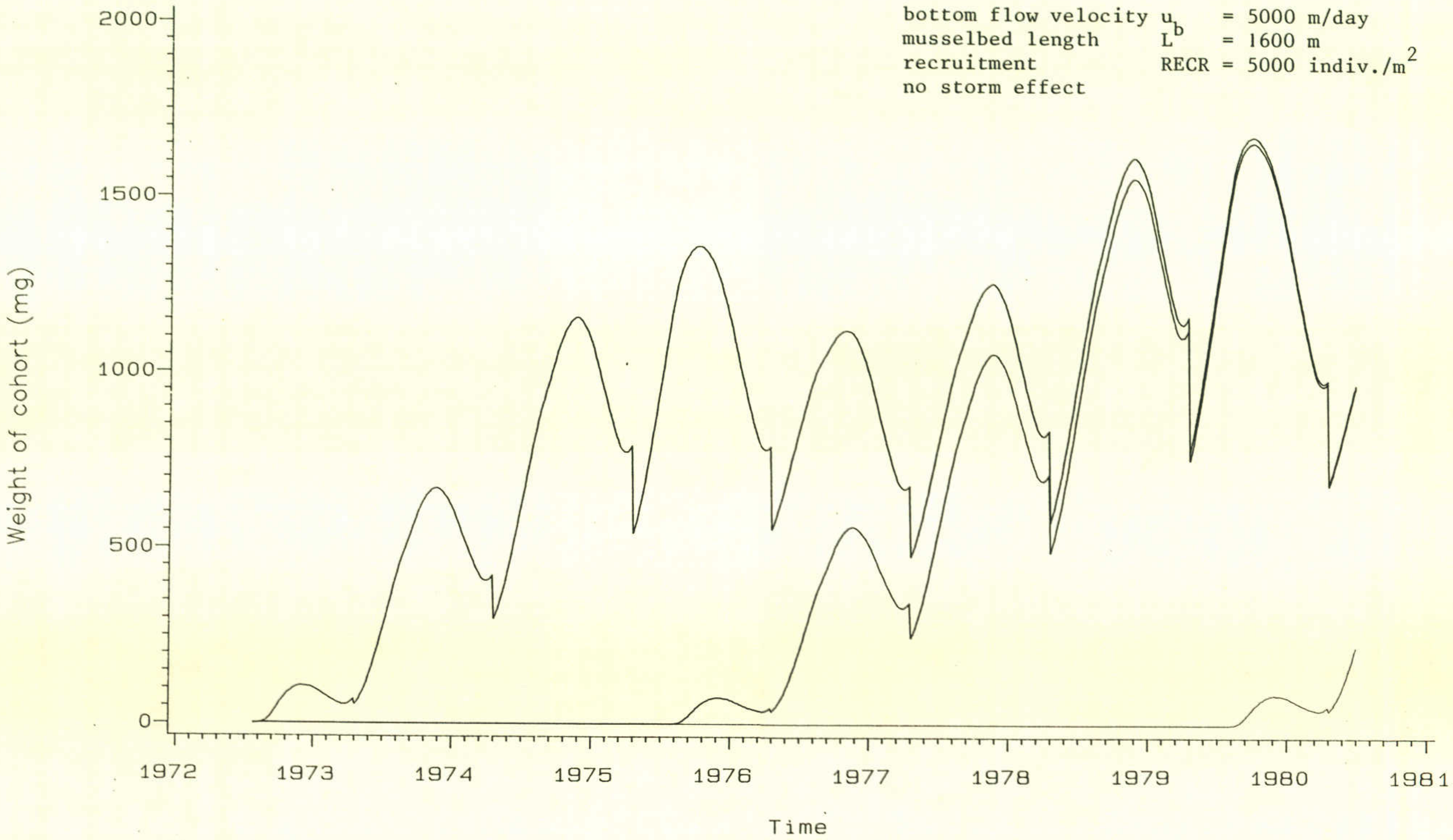


Figure 26

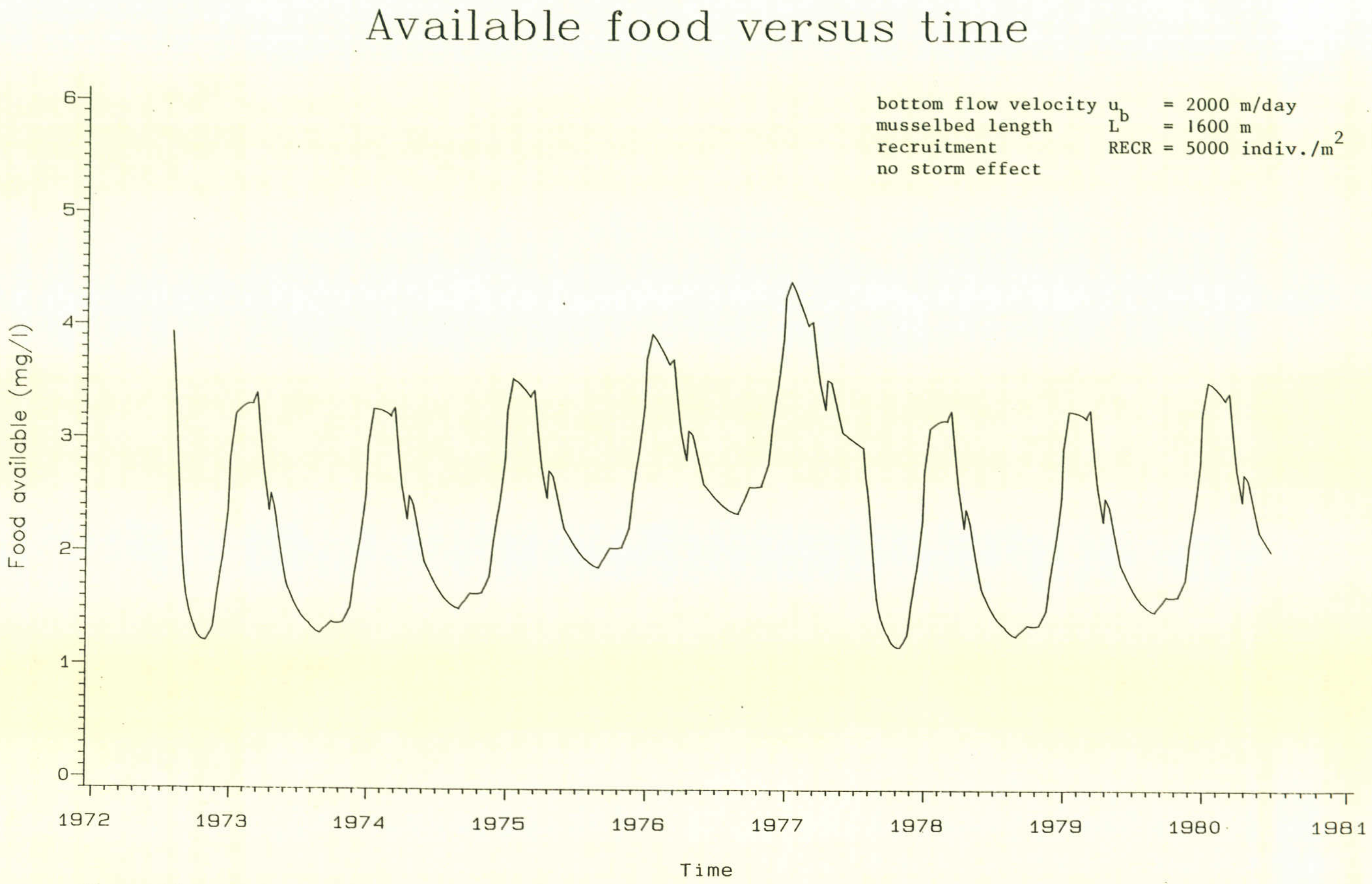

Available food versus time
bottom flow velocity u_b = 2000 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Food available (mg/l)
0
1
2
3
4
5
6
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 27

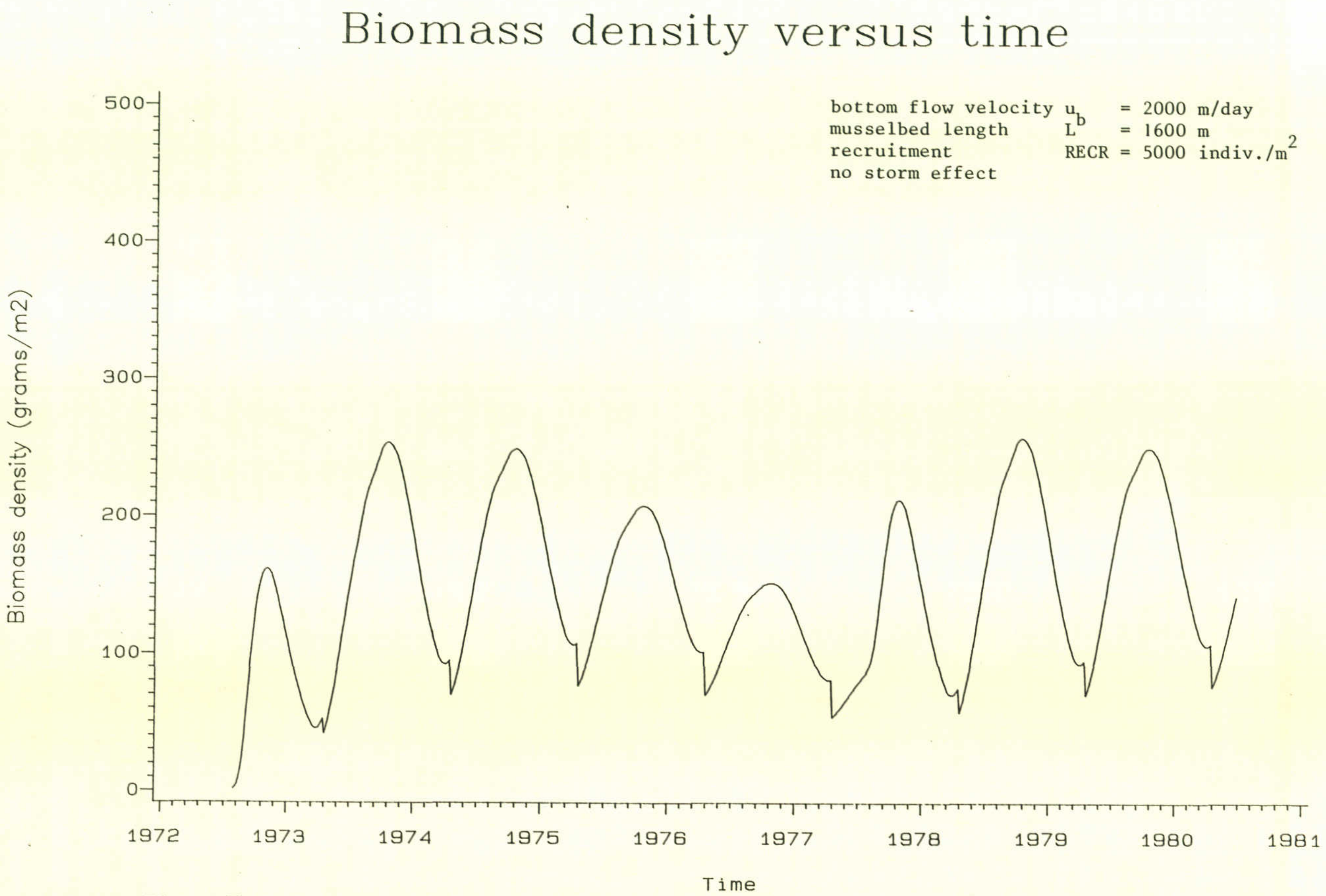

Biomass density versus time
bottom flow velocity u_b = 2000 m/day
musselbed length L^b = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Biomass density (grams/m2)
500
400
300
200
100
0
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 28

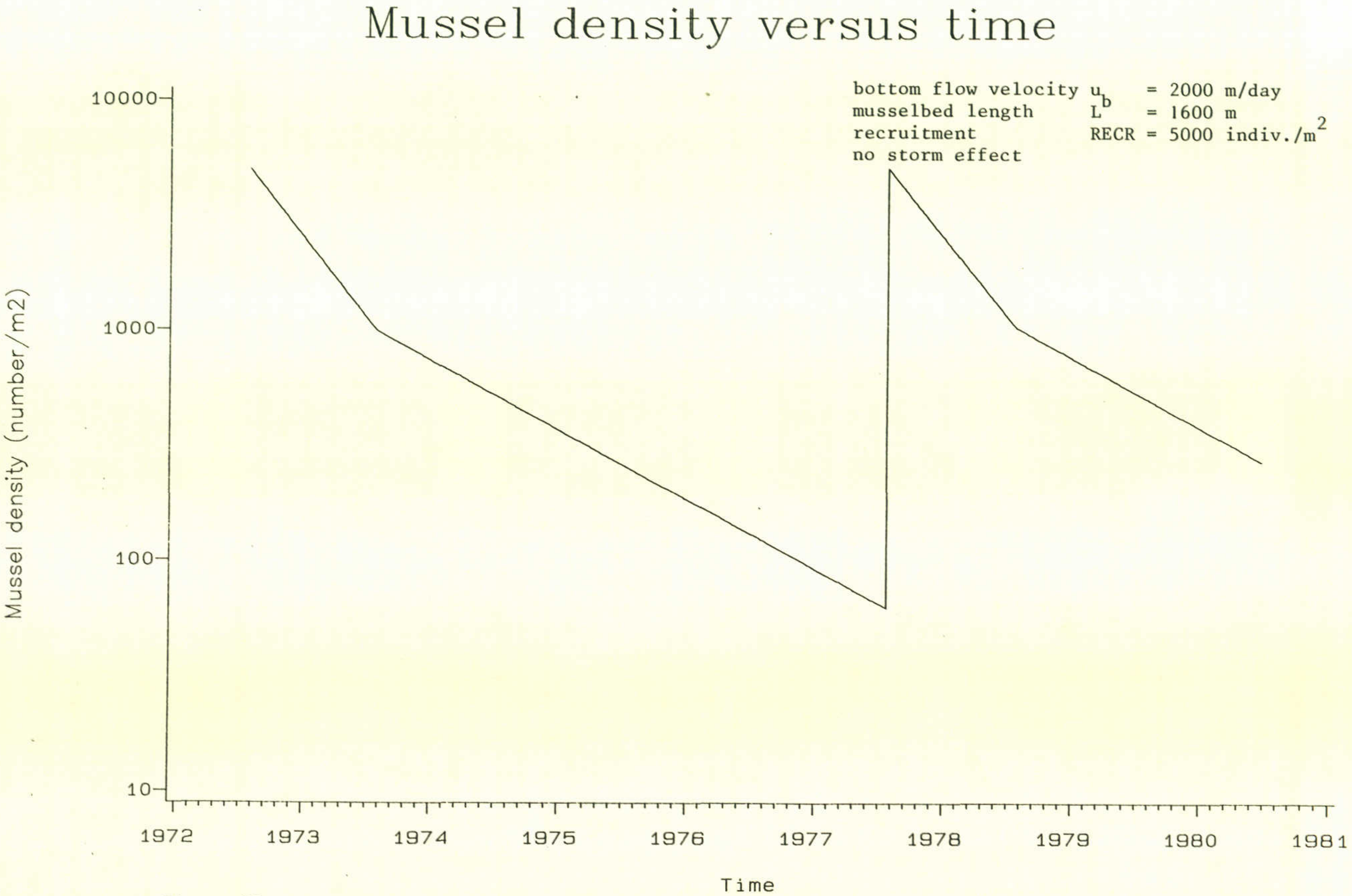

Mussel density versus time
bottom flow velocity u_b = 2000 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Mussel density (number/m2)
10000
1000
100
10
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 29

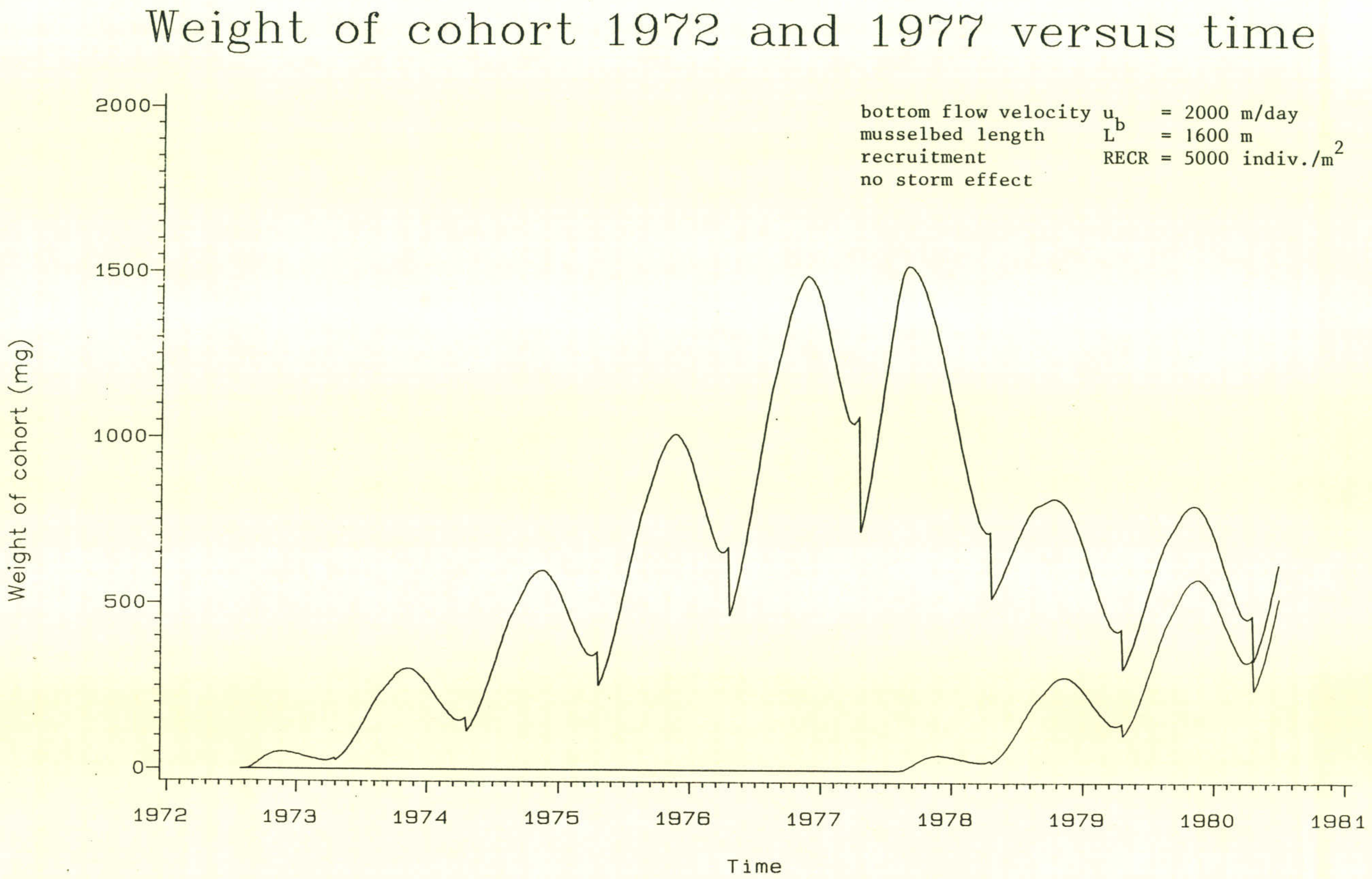

Weight of cohort 1972 and 1977 versus time
bottom flow velocity u_b = 2000 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Weight of cohort (mg)
2000
1500
1000
500
0
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 30

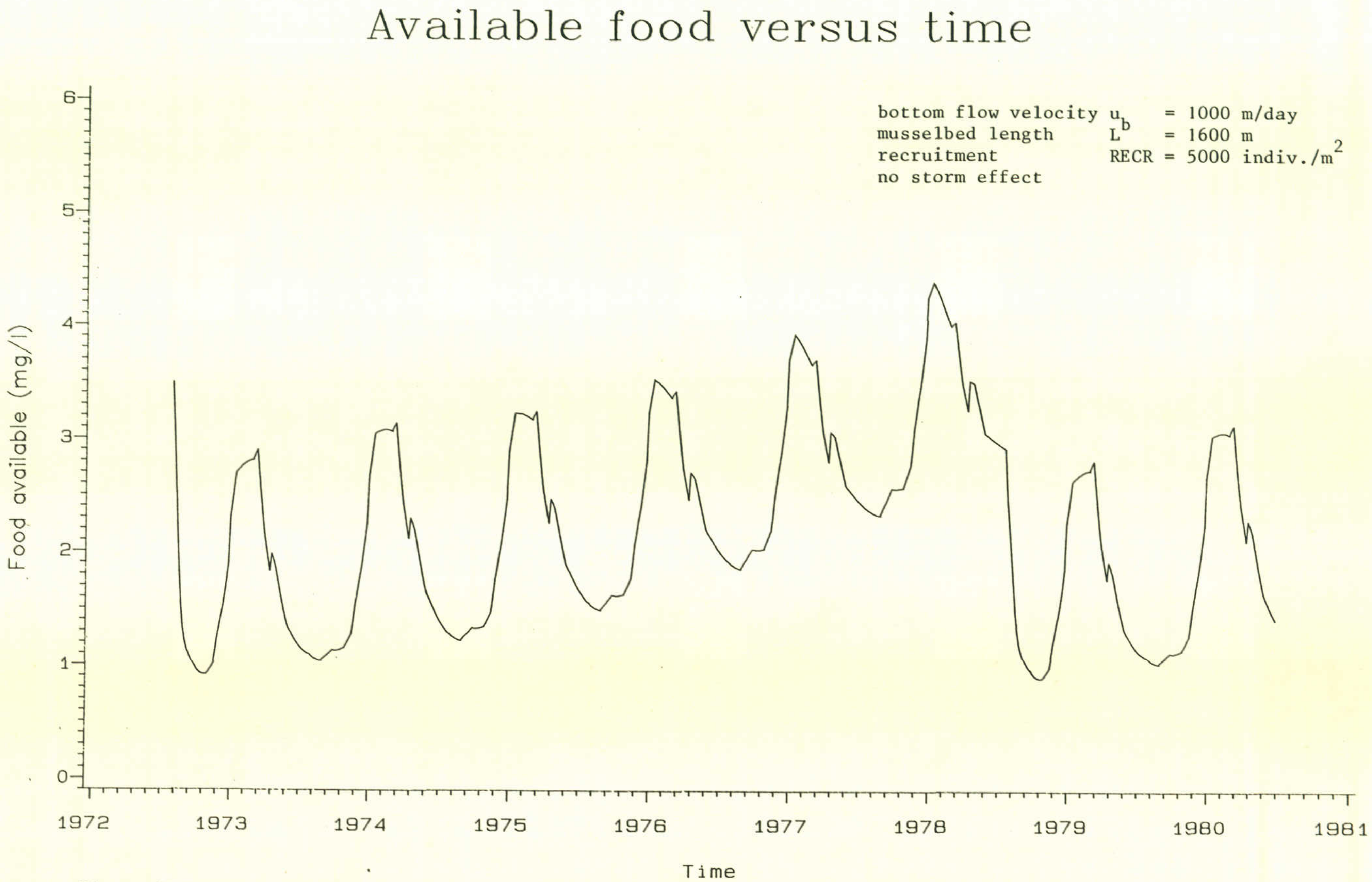
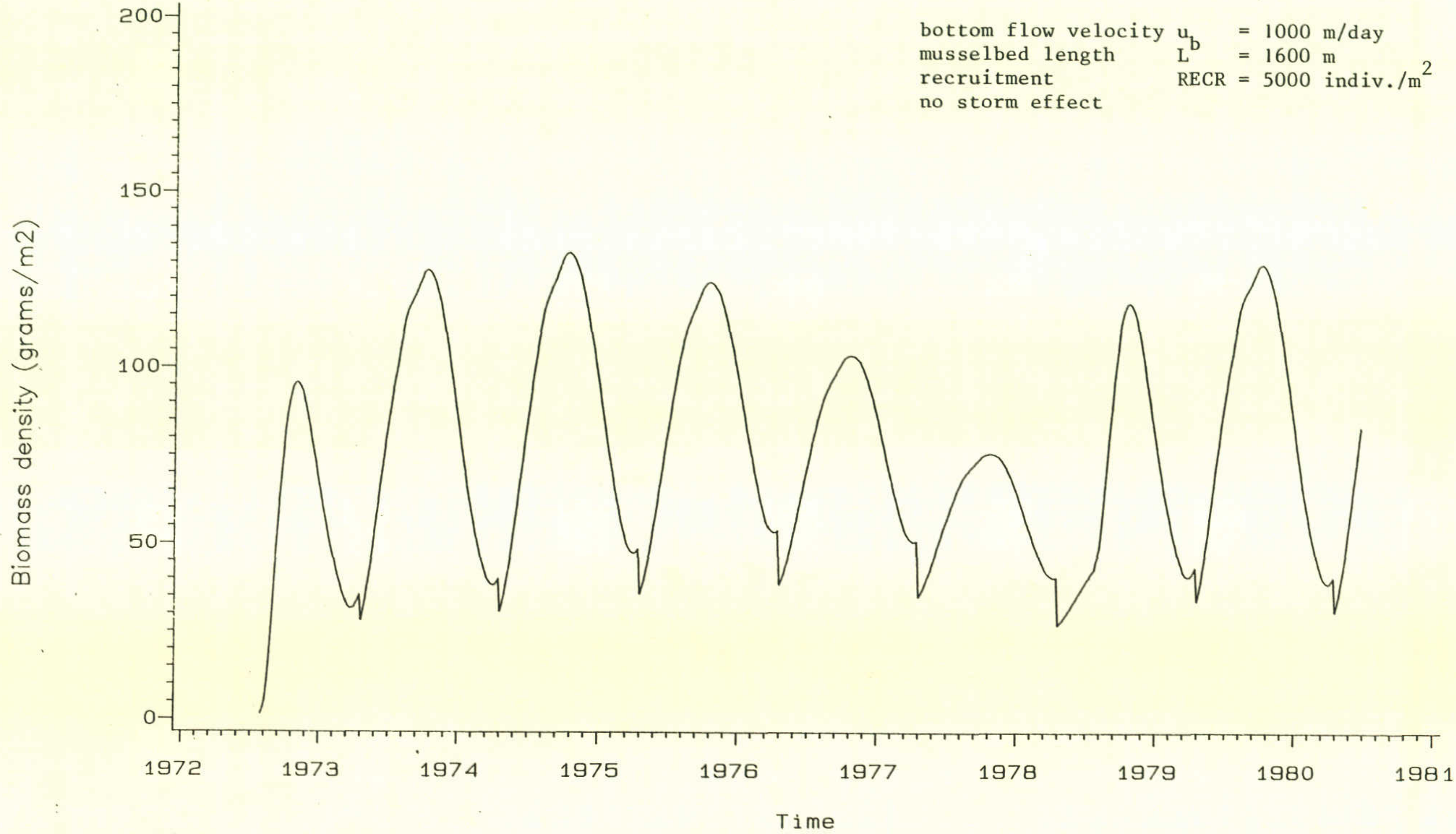

Available food versus time
bottom flow velocity u_b = 1000 m/day
musselbed length L^b = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Food available (mg/l)
0
1
2
3
4
5
6
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 31



Biomass density versus time

Figure 32

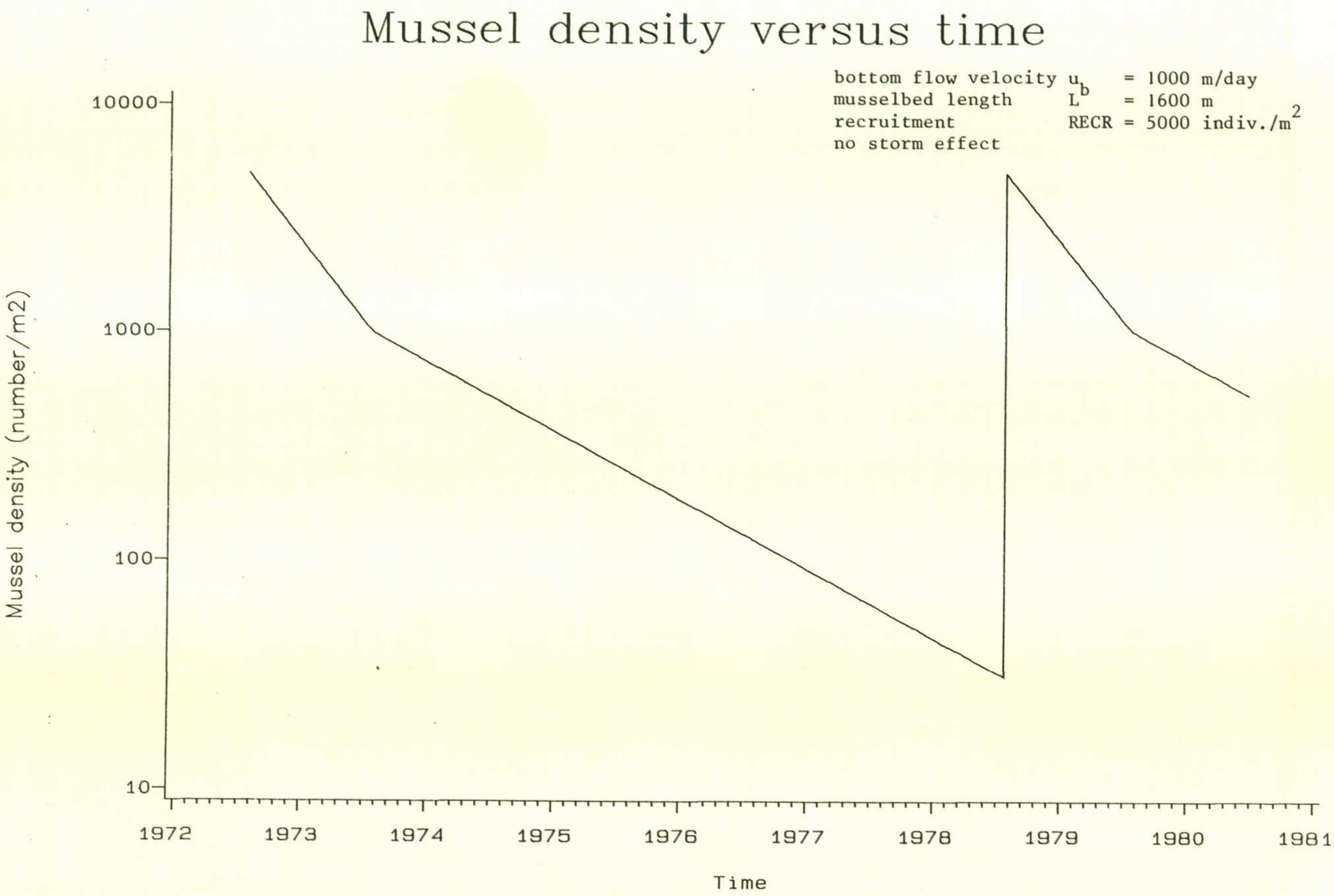
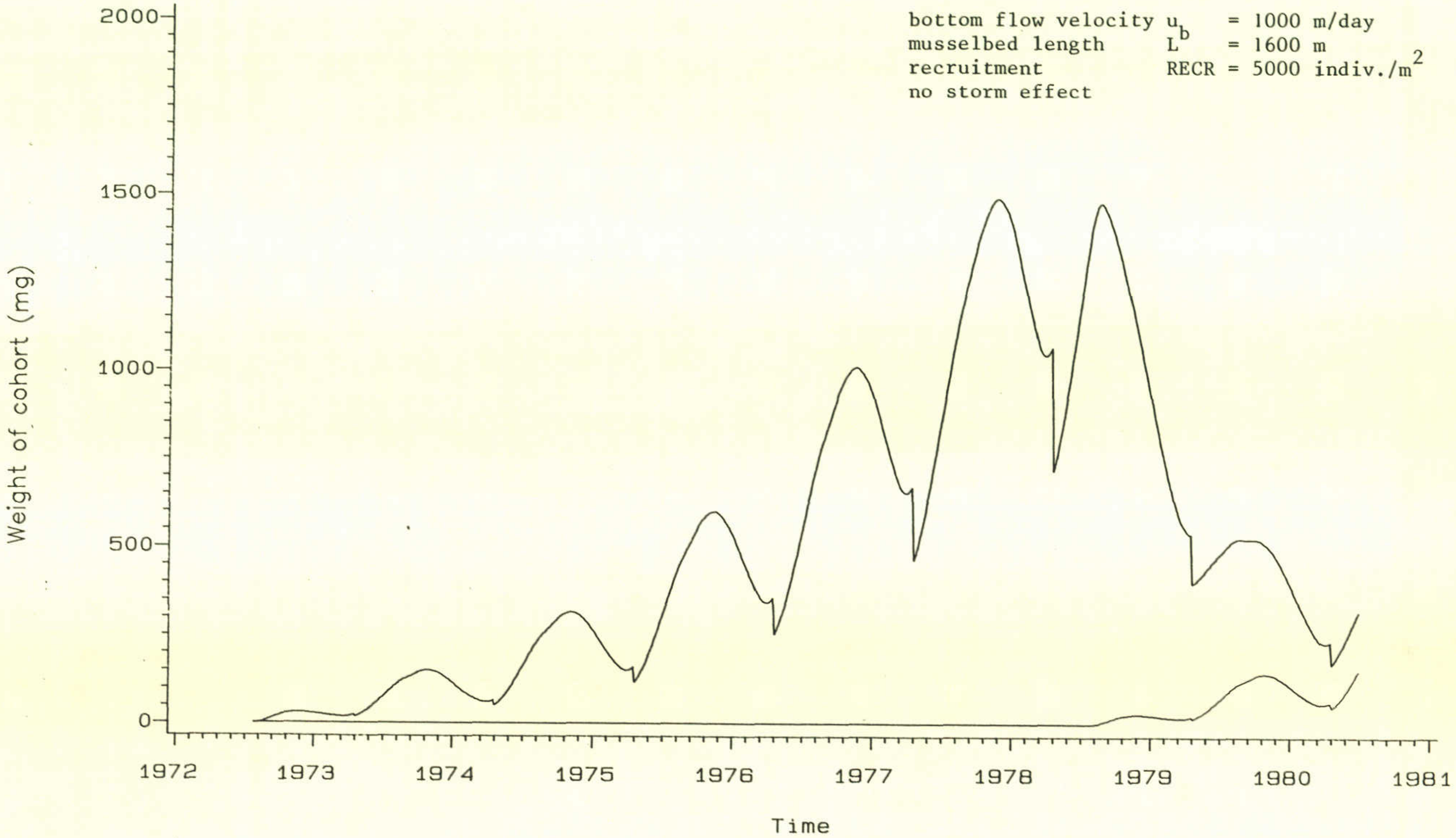
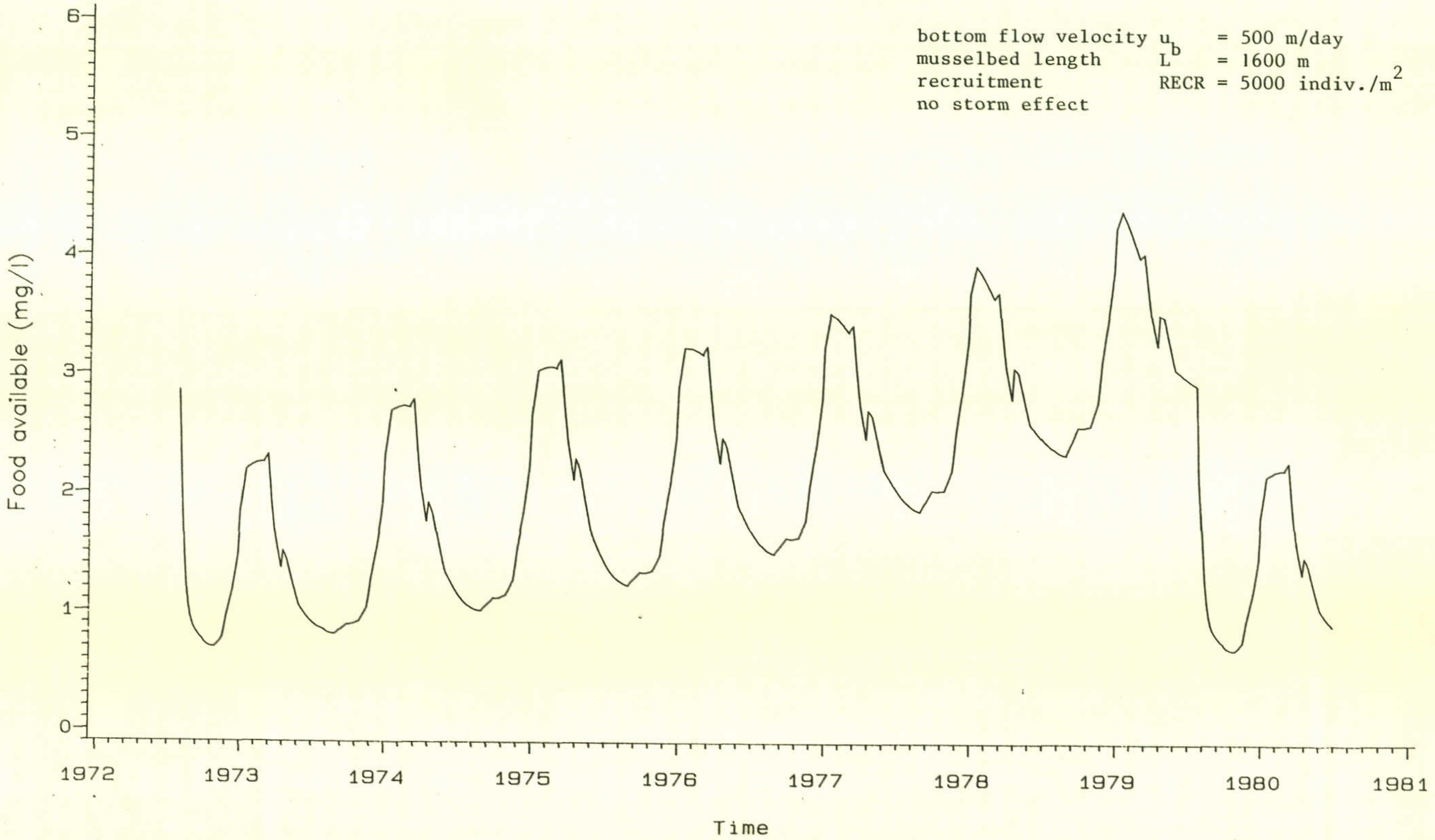

Mussel density versus time
bottom flow velocity u_b = 1000 m/day
musselbed length L^b = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Mussel density (number/m2)
10000
1000
100
10
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 33



Weight of cohort 1972 and 1978 versus time

Figure 34



Available food versus time

Figure 35

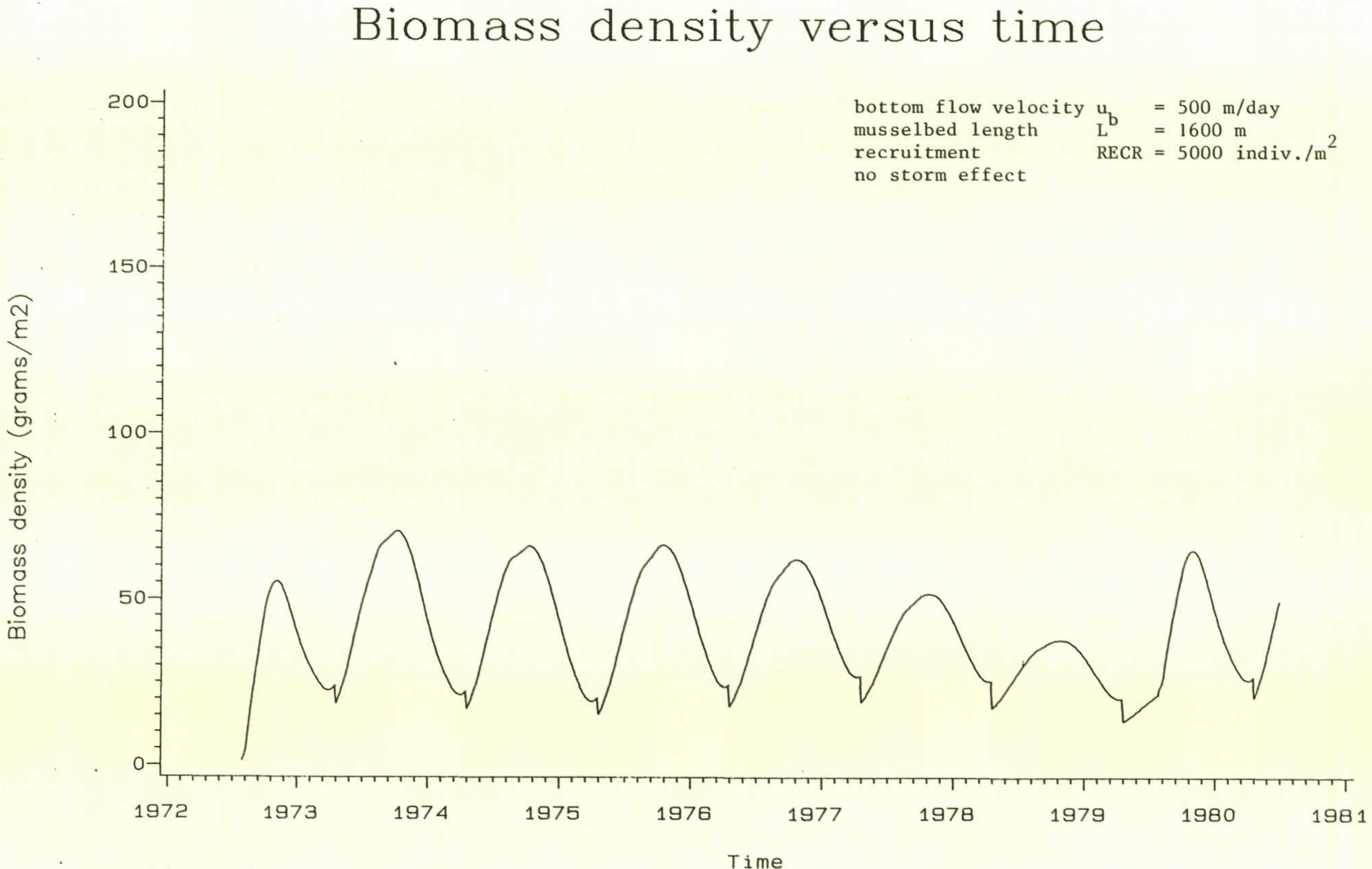

Biomass density versus time
bottom flow velocity u_b = 500 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Biomass density (grams/m2)
0
50
100
150
200
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 36

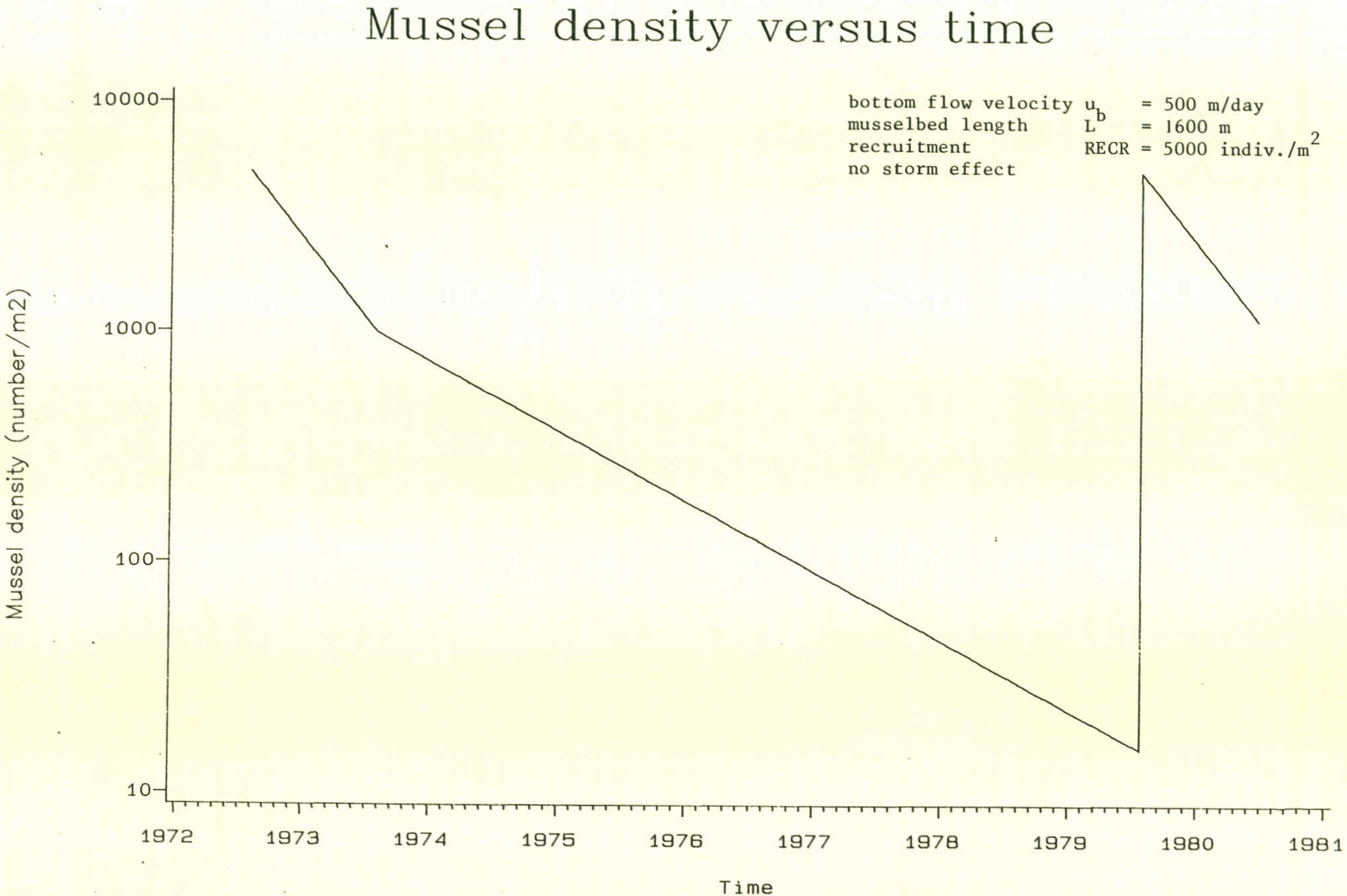

Mussel density versus time
bottom flow velocity u_b = 500 m/day
musselbed length L = 1600 m
recruitment RECR = 5000 indiv./m^2
no storm effect
Mussel density (number/m2)
10000
1000
100
10
1972
1973
1974
1975
1976
1977
1978
1979
1980
1981
Time

Figure 37


Weight of cohort 1972 and 1979 versus time

Figure 38

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