Services du Premier Ministre
Programmation de la Politique scientifique
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ACTIONS DE RECHERCHE CONCERTEES

ACTION INTERUNIVERSITAIRE

OCEANOLOGIE

Rapport final

Volume 4

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Programmatie van het Wetenschapsbeleid
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BELGIE

GECONCERTEERDE ONDERZOEKSACTIES

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Artemia

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TRENDS IN NURSERY REARING OF BIVALVE MOLLUSCS

Christine CLAUS

Abstract.

Nursery rearing of bivalve molluscs, as the intermediate step between the controlled production of larvae in commercial hatcheries and the growth-out in the wild, is a practice which is receiving more and more attention in mollusc farming. The purpose of nursery rearing of bivalves is to culture cultchless spat of a few millimeters in size, up to 1-2 cm, in a minimum of time, in densities as high as possible, and at minimal costs and risks.

In the last decade various technologies for nursery culturing, indoors as well as outdoors, have been developed at different places, ranging from suspended culture in the open sea to controlled onshore culture in upwelling cylinders. This paper reviews the different systems developed until now, with special emphasis on one of the key problems, namely the supply of the right amount of suitable food for the juvenile bivalves, in function of flow rates, stocking densities, and temperature.

The growth and mortality rates of *Ostrea edulis*, *Crassostrea gigas*, *Venerupis semidecussata*, *Mercenaria mercenaria*, *Argopecten irradians* and *Crassostrea virginica*, under nursery conditions is discussed. A few considerations are made with regard to the economic aspects of nursery operations.

1.– Introduction.

Nursery rearing of bivalve molluscs is an intermediate step between the controlled production of larvae in commercial hatcheries and the growth-out of the shellfish in the wild.

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Hatcheries for oyster and clam seed are in operation and have become an essential part of the shellfish farming. Each year millions of juvenile bivalves are produced artificially by known methods and techniques. A review is given by Loosanoff and Davis (1963). Without over-simplifying the matter, one can say that bivalve hatcheries have reached a level at which the developed techniques only need to be optimized.

As a matter of fact, the problems came from maybe an unexpected angle. Indeed, some hatcheries have failed due to the unexperience of growers in handling small cultchless seed and their unwillingness to develop new techniques and equipment. Generally, ongrowers prefer seed of 8-10 mm and larger, instead of the 3 mm spat sold by the hatcheries. This indeed simplifies the counting, the maintenance and reduces the mortality and tray losses. Rearing spat to this size puts, however, considerable pressure on the hatcheries. It is clear that for economic reasons, industrial mollusc hatcheries can barely scale up their very expensive indoor algal production to fulfil the increasing food demands of the ongrowing spat.

This gap between hatchery and on-growing can be bridged by the so called nurseries. In these nurseries, which may considerably vary in their approach to the problem, large quantities of bivalve postlarvae are stocked in protected conditions. These nursery conditions are less sophisticated than those in the hatchery. Therefore the spat can be held longer and at less cost, until it is sold to the ongrowers. The nursery furthermore ensures a more gradual transition from the hatchery to the natural environment, and thus improves the chances of survival. In this regard Bayes (1981) made the following statement : "It is the development of the nursery stage, that has made a sound business of the hatchery production of bivalves". While Le Borgne (1981) reported : "the nursery culture of postlarvae is the key for the further development of bivalve hatcheries".

Various authors consider that successful oyster culture should be based on five subsequent stages, and that it is particularly important not to push any one stage past its limits (Gerard, 1976; Bayes, 1979). This five stages are :

1. the hatchery operation in strictly controlled conditions and leading to the production of stock of maximum 5 mm;
2. a nursery stage with ongrowing in running sea-water under protected conditions to a size of approximately 10 mm;
3. ongrowing in the sea in trays. This stage is considered economically feasible up to a size limit of approximately 25 mm, above this size a less costly method of ongrowing to maturity is essential;
4. ongrowing to maturity using bottom-laying or alternative methods;
5. hardening before marketing by exposure between tides.

In order to illustrate the complexity of the nursery problem and the numerous ways in which scientists as well as commercial people are trying to find solutions to it, this paper briefly reviews the present state of the art of nursery rearing systems.

2.– Biotechnical aspects of nursery culturing and culture devices.

2.1.– *Offshore culturing.*

The biological requirements which must be met by any method for handling young spat, concern primarily the feeding. Bivalves feed by filtering sea-water and extracting mainly phytoplankton. To what extent other solid or soluble substances in the water contribute to the bivalves' diet as well, is not taken into consideration here. To sustain growth of the oysters, they need to be kept in a constant flow of plankton-rich sea-water. This requirement is normally fulfilled in the estuaries in the temperate climatic zone. Consequently to date, nursery culturing is mostly performed with the natural phytoplankton present in the sea-water being the sole source of food for the juvenile bivalves.

The most classic and the oldest technique for rearing post-larval bivalves is simply to place the cultchless seed in some kind of stocking device in a suitable environment. Since seed oysters of 2-3 mm may suffer high mortality, special techniques must be employed to ensure maximal growth and survival. Several methods can be used to achieve these aims :

- intertidal racks arranged on structures on the sea shore;
- trays suspended near the surface from rafts moored in open water;
- trays suspended in mid-water on long lines without costly floating structures;
- upwelling systems.

Shore-based systems can be reached only at low tide, while rafts are usually accessible at all times. Rafts, however, are costly to build and maintain, which must be considered in relation to the value of the crop. In the shore based systems, the position of the racks with regard to the tidal height is critical, since it is a compromise between continuous total immersion, when maximal growth is obtained, and sufficient periods of exposure to enable servicing. For the Pacific oyster *Crassostrea gigas* (Thunberg) it has been shown that exposure to air in the range of 10 to 30 % of the time, led to a marked reduction in growth rate (Spencer et al., 1978).

Plastic meshes are used to retain the oysters in trays which vary widely in design and size. Prefabricated trays which nest on one another have recently become available, and although they are more expensive than light mesh trays, their durability may make them attractive for long-term use.

The majority of the oyster growers, particularly those concerned with Pacific oysters, nevertheless uses rafts of one form or another. The waste of capital in building too large a raft, or cramping of stock on too small a raft, is to be avoided. These problems can be eliminated by using modular designs in which the raft consists of a number of small separate units (E. Hoet, personal communication). If the units are too small an auxiliary boat may be needed for servicing, because the raft does not represent a stable working platform.

The stocking device for oysters must be well designed, to allow an adequate water flow over and around every individual animal, and yet offer protection and support. A few examples of devices for the suspension technique are, the stacked wooden trays with mesh bottom (Spencer and Gough, 1978; Neudecker, 1981), the self stacking plastic trays (Davidson, 1974), the Japanese lantern-nets (Ley, 1978; Shaw, 1981), the "casiers-tiroirs" (Lucas and Gerard, 1981), the plastic mesh bags (Yelf, 1978), and the prefabricated plastic circular trays with a central suspending rope (George, 1975). Bunching of bivalves, particularly of the small spat may be avoided by keeping the support surfaces as flat and horizontal as possible.

Holding small spat in trays represents a particular problem, because the fine retaining meshes tend to become blocked very quickly. In silt-loaden water, fine mud gathers on the meshes, and where siltation is not the problem, biofouling usually is. Therefore, trays with fine mesh may require servicing every few days. This is usually done by periodic air drying of the trays, followed by vigorous flushing with a high volume and high pressure water stream. This method, although efficient, adds significant cost to the grow-out procedure.

Recently trays have been developed with a removable mesh curtain to surround a stack of circular trays. These curtains are easily replaced whenever they begin to suffer from fouling (George, 1975). Alternative solutions need further investigation. Research has been carried out on the biological fouling control in which natural enemies, such as crabs are used to eliminate the biofouling material – usually mussels – (Hidu et al., 1981). Reasonable success has been booked by replacing the plastic nettings with nettings in a Cu-Ni alloy, which greatly inhibits the biofouling on the trays (Huguenin and Ansuini, 1975). Bio-accumulation of these heavy metals in the juvenile shellfish is, in some cases, important, but has been proven to be reversible (Benijts, personal communication).

The classical suspended culture of bivalves in trays is a monolayer practice requiring more than a hundred times as much tray space as compared to the three-dimensional (3D) upflow systems which has been developed for the rearing of spat. The idea behind the upflow technique, is to increase the water flow-rates through the cultures and to meet the food requirements of the shellfish by circulating larger volumes of food-containing medium through the cultures.

The upflow system from which all modern spat-rearing systems have been derived (Bayes, 1979, 1981; Le Borgne, 1980, 1981; Guerrero et al., 1981; Lucas and Gerard, 1981; Williams, 1981) has originally been developed by W. Budge (1970, US Pat. n° 3526209). Originally it has been designed to operate with pumped sea-water. The water is forced to flow upwards through the container with a mesh bottom holding the oysters. The water leaves the container through an overflow at the top of the cylinder, and eventually can be recycled several times.

The advantage of such upflow systems is that they allow culturing of spat piled up in several layers. The young oysters do not stick to the trays, and the faeces and pseudofaeces are not accumulated upon or between the spat and thus do not clogg the meshes of the bottom. A few commercial operations in Scotland and at Guernsey, Channel Islands, apply the upwelling principle in their offshore nursery (Lintell, 1980, 1981; Williams, 1981).

Both systems consist of a raft with a series of upwelling units and air compressors supplying the air flow that operates the airlifts which suck water up through the oyster bed.

This system appears to have many advantages as compared to the ongrowing of seed in trays, especially as far as man-power for maintenance is concerned. An additional benefit can be made by working in sheltered conditions in a natural or man-made closed basin connected to the sea by means of a sluice allowing the controlled exchange of water with the sea at high tide. Both the temperature and the primary production of such enclosures are somewhat higher than in the open sea which results in a faster growth of the spat. Another new application of the upflow technique in the natural environment, is based on the tidal action (Spencer and Hepper, 1981).

2.2.– *Land-based operations using natural phytoplankton.*

Because of the rather difficult manipulation of rafts and floating devices, it is preferable to operate an onshore unit with a continuous flow of natural sea-water through the culturing devices.

If the nursery is located in an area where phytoplankton is abundant, the sea-water can be pumped directly through the nursery. From the technological point of view, two different nursery systems are interesting to cite.

First, the raceway system used in Milford (U.S.A.) and which Rhodes et al. (1981) describe as "an ideal compromise between costly controlled systems and uncertain field plants", and second, the gravity-fed system designed as an extension of the storm-surge barrier in the Netherlands, namely the project MARIOS developed by Drinkwaard (1981).

Persoone and Claus (1980) and De Pauw (1981) emphasized that in most cases the primary production in open sea, even in sheltered areas, is far from sufficient to fulfil the nutritional requirements of several millions of bivalve spat in an onshore nursery-plant with natural sea-water being the sole food source. Therefore, impounding the water and eventually adding fertilizers to the water to induce phytoplankton blooms, is a technique which has been adopted by several commercial firms in Europe (Le Borgne et al., 1978; Bayes, 1981; Lucas and Gerard, 1981; Rabeux, personal communication). The bivalve spat is kept in appropriate culturing units, mostly upwelling cylinders, through which the pond water is directly pumped. Placing the nursery unit proper in a greenhouse can be favorable for the bivalves' growth (Lucas, 1976). Recirculation of the pond water in various percentages is also becoming a more widely spread practice. Another attempt to take full advantage of the eutrophic sea-water was made by Hughes-Games (1977) who introduced oyster trays in the draining channels of a marine fish-culturing station in Israel.

In all cases, however, the operation remains entirely dependent upon incontrollable environmental conditions, and therefore suffers from important differences in growth rate of the bivalve spat, which can be related to the variation in the natural phytoplankton density. Uncontrollable blooms of unsuited or even toxic microalgal species or the excessive growth of macroscopic algae in the pond competing for the nutrients, may be disastrous for this kind of nursery operation.

2.3.– *Land-based operations using cultured phytoplankton.*

With all the shortcomings of the previous systems in mind, a fair number of people, mainly scientists, working in the field of nursery rearing of bivalves, have tried to develop more controlled culturing-systems in which supplemental feeding was given to the bivalves.

The emphasis has been on the use of live algae. Besides its close resemblance to the natural diet, the advantages of this food are that it remains in suspension, and that the cells which are not eaten do not decay and pollute the water. For commercial application, however, the disadvantage of an algal diet resides in the fact that the production of a sufficient quantity of algae is technically the most difficult part of the operation, and when used to feed juveniles it becomes relatively costly (De Pauw, 1981).

Since a long time many attempts have been made to induce blooms of natural phytoplankton in algal tanks of various dimensions, by adding agricultural fertilizers to the sea-water. This technique has been developed and improved worldwide by many mariculturists. Although it looks very easy to do, it has been proven that this method is only reasonably successful, if one keeps a large number of parameters under control. "Unmanaged water is frequently better than mismanaged water" (Bayes, 1979). Details on this subject were given by De Pauw (1981). Recent experiments on nursery rearing of bivalve spat by means of induced blooms were described by Lucas (1976), Riva and Lelong (1978, 1981), Guerrero et al. (1981), Mercer (1981a,b), reflecting the latest evolution in the matter.

A classic example of mass production of marine microscopic algae in outdoor ponds to feed commercially important bivalves, is the series of experiments carried out by the research team of Ryther in the Woods Hole Oceanographic Institution in Massachusetts, U.S.A. (Ryther et al., 1972, 1975; Mann and Ryther, 1977; Mann, 1979a,b; Mann and Taylor, 1981). In all these experiments the algae were cultured in six ponds of 15 m diameter. The cultures were enriched with a continuous addition of secondary treated sewage effluent. The harvested algae overflowed into concrete raceways containing the shellfish. The shellfish were held in plastic trays and the water was heated to 15 and 20°C.

More or less based on this model our laboratory very recently built an onshore nursery rearing-system at pilote scale at the border of the Sluice Dock in Ostend at the Institute for Marine Scientific Research (IZWO). It consists of four outdoor algal tanks of approximately 100 m^2 surface and an indoor nursery-unit. Blooms of natural phytoplankton are induced by adding agricultural fertilizers. The nursery proper consists of four tanks with rows of eight upflow cylinders (figs 1 and 2).

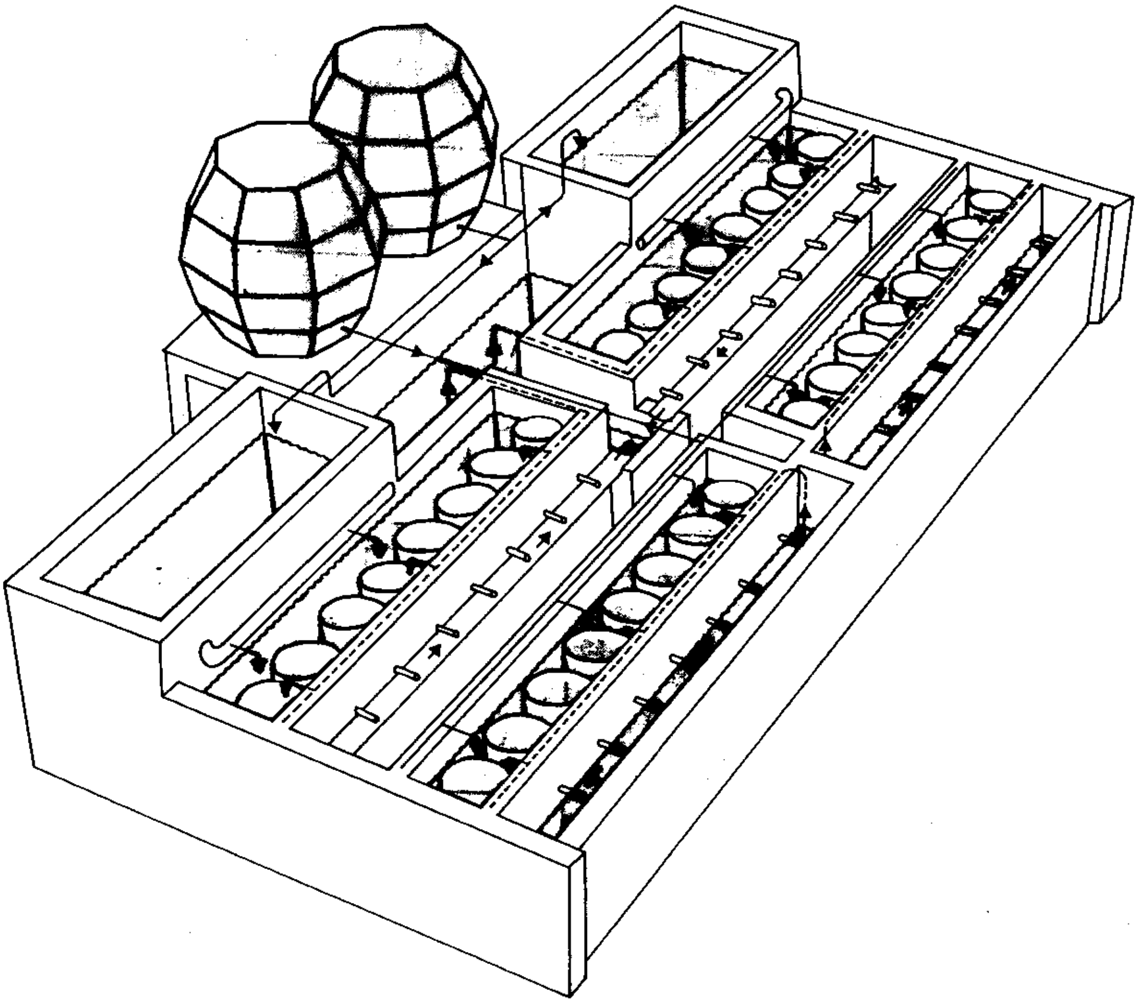

fig. 1.

General schematic view of the experimental indoor bivalve nursery at the Institute for Marine Scientific Research (IZWO), Ostend

Sea-water is pumped into two constant-head devices from which the water is distributed by gravity into the four rearing tanks. For two rearing tanks the sea-water flows through an intermediate heating tank. Heating occurs indirectly by means of an electric boiler and two radiators. The algal suspension is pumped into a separate storage tank from which it is distributed by gravity to the rearing tanks at a maniable constant flow-rate. The outflowing sea-water runs through a reservoir from which it can eventually be recycled through the cultures. The outflowing

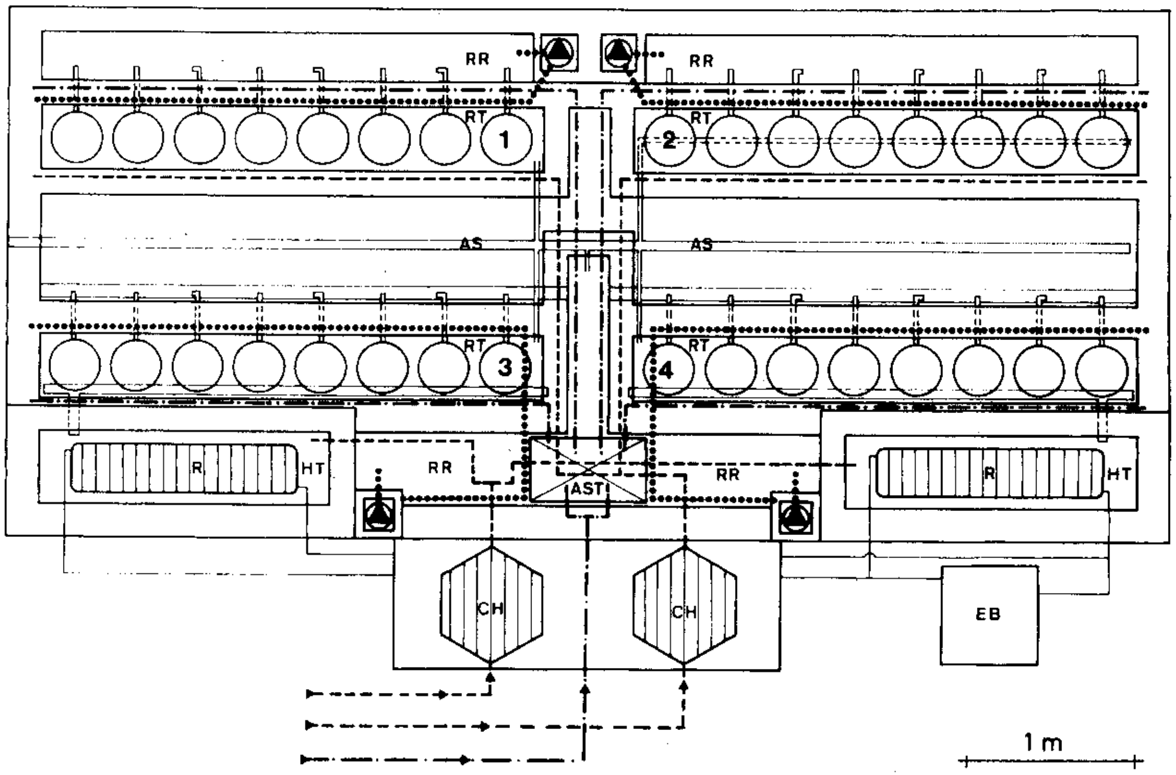

fig. 2.

Scheme of the indoor bivalve nursery at the Institute for Marine Scientific Research (IZWO), Ostend CH : constant head; HT : heating tank; RT 1, 2, 3, 4 : rearing tanks; RR : recycling reservoir; EB : electric boiler; R : radiator; AST : algal storage tank; AS : air supply; ◉ : recycling pump; — — —: water supply; — · — ·: algal supply; ………: water recycling heated sea-water is used to preheat the inflowing fresh sea-water. The spat is stocked in upflow cylinders with a mesh bottom.

The whole system is conceived in such a way that the influence of the variation of many parameters such as temperature, flow rate, feeding rate, stocking density, etc. can be assessed. The ultimate goal of this pilot plant is to make a cost benefit analysis of an industrial nursery utilizing a heated effluent.

A second trend in the production of microscopic algae as food source for nursery bivalves, relies on the completely controlled production of specific phytoplankton species. This implies keeping stocks of monospecific algae, progressive inoculation of cultures of increasing volumes, and controlled culturing conditions in either indoor or outdoor conditions.

From the many laboratory experiments with young bivalve spat fed different monospecific algal suspensions in various concentrations and mixtures, many interesting conclusions with regard to the nutritional value of these algal species could be drawn. These are directly applicable in the large-scale rearing systems. A review of the literature on this topic was given by De Pauw (1981).

Why the different algal species vary in their food value is not yet understood, but since there is such an important difference in food value, it is not surprising that the mass culturing of the most suitable species for bivalves has been tried out under indoor as well as outdoor conditions in various places (Walne, 1970a,b).

A few experimental and commercial installations are described because they brought some important innovations in the concept and the technology of the bivalve nursery. In the University of Delaware, U.S.A., an experimental closed-cycle controlled mariculture system has been developed, with the aim to raise bivalve molluscs from egg to market size in a recirculating system on a diet of monospecific algae *Thalassiosira pseudonana* and *Isochrysis galbana*. These algae are cultured in a large greenhouse in circular tanks of 9.5 m^3. The algal suspension is pumped continuously through the oyster growing-tanks. Oysters and algal cultures are grown at the same temperature of 18 to 20°C. A cost benefit can be made if the heated sea-water and the unassimilated algal cells can be conserved and recycled. There is also a potential value in recycling the nitrogen and phosphorus by recycling the overflow of the oyster tanks back to the algal cultures. The levels of the micronutrients for the algal culture and of calcium for the shellfish need to be monitored and adjusted (Pruder et al., 1978).

The water quality is one of the critical factors for a controlled bivalve rearing-system based on monospecific algal cultures. In most cases surface sea-water must be filtered or centrifuged to remove the undesirable organisms, and in most cases the water is sterilized. This kind of water treatments can be minimized if one utilizes salt well-water, free of pollutants, undesirable species, diseases, and predators harmful to the shellfish. This is how the Cultured Clam Corporation in Dennis, Massachusetts, U.S.A., operates. The hard clam *Mercenaria mercenaria* is grown on pure algal strains cultured in large outdoor tanks. Similarly, in two commercial plants in Hawaii *Crassostrea gigas* is reared up to commercial size on algae mass-cultured in open ponds of 2 500 m^2. From the engineering point of view, the design of the technology used in Aquatic Farms Ltd. in Hawaii is remarkable. The trenches receiving the oyster trays have been built as a cascade. Each trench is located slightly below the level of the previous one and slightly above the next one. The phytoplankton suspension flows over the oyster trays, is forced down by gravity through each stack of trays and then flows to the next trench where it is enriched again with new phytoplankton to bring the concentration back at the original level (Burzell, 1978; Pryor, 1978).

The idea of coupling a mollusc mariculture plant with an OTEC plant (Ocean Thermal Energy Conversion) has been studied in St Croix, Virgin Islands in the Caribbean Sea (Roels et al., 1976). Deep-sea water, very pure and rich in nutrients, is pumped continuously from 870 m depth into two concrete pools in which unialgal cultures of diatoms are grown. The algal cultures are pumped continuously into the shellfish tanks where several species of oysters and clams have been raised up from spat to market size in approximately one year (Sunderlin et al., 1975, 1976; Rodde et al., 1976).

Unfortunately, in none of these four large-scale operations, the upwelling system has been used to stock the bivalve spat. Undoubtedly this sytem would better reduce the problem of the large quantities of faecal material sticking to the trays than some of the sophisticated devices that were used (Langton et al., 1977).

3.– Mortality rate in the nursery.

It is clear that seasonal variations in the parameters of the natural environment are reflected in both the growth and the mortality curves of the bivalve populations.

Walne (1974) stated that when very young *Ostrea edulis* L. spat of less than 1 mm is moved outside, whatever the season, mortality is usually high, and mortality is always high, when spat is moved outside in the winter and early spring, whatever its size. These mortalities are attributed to the large temperature shocks. Spat grown in cooler water, has a relatively higher meat content and can better withstand the transition to the cooler outdoor conditions.

The seasonal mortality of newly planted spat in their first month on a raft, has been studied by Spencer and Gough (1978). These authors showed that for *Ostrea edulis* the mortality is maximal in the warmest months of the year, and for *Crassostrea gigas* in April and May.

In some of our own experiments similar phenomena were observed. Other factors than temperature must be taken into consideration, such as the density and the species composition of the phytoplankton. In our experiments the summer mortalities of both oyster species in the Sluice Dock in Ostend were attributed to the consecutive shocks of high levels of free ammonia at the end of the day as a result of the very important photosynthetic activity in this eutrophic water, and the nearly complete depletion of dissolved oxygen during the night caused by respiratory activity.

Blooms of toxic algal species such as toxic dinoflagellates and of *Phaeocystis* and to a certain extent *Chlorella* can cause severe mortality of the spat (Loosanoff and Davis, 1963; Walne, 1976). Summarizing a number of experience papers on the rearing of bivalve spat in the natural environment, one can say that mortality is unpredictable and thus hard to control. An average mortality of 50 % is not unusual. Mortality in a controlled onshore nursery installation is generally far less. From literature data, the averaging mortality rate during the nursery stage is expected to be 10-30 % for *Ostrea edulis*, 5-25 % for *Crassostrea gigas*, 20-60 % for *Mercenaria mercenaria*, 10-40 % for *Venerupis semidecussata* Adams and Reeve, 30-50 % for *Argopecten irradians* Lmk, and 5-20 % for *Crassostrea virginica* (Gmelin).

4.– Growth performances.

All the nursery practices described above result in different growth rates of the various bivalve species. In the systems used in the natural environment in the temperate climate zone, the growth of the shell and the soft tissues of the spat is limited to the warmer period of the year. The growing season usually starts in April and ends in October. As established by laboratory studies, in which the natural sea-water was heated during the winter, temperature is not the only growth-limiting factor during this time of the year (Malouf and Breese, 1978; Clause et al., 1981; Malouf, 1981). The amount of available food is at least as important. In nature these two environmental requirements for growth may often be mutually exclusive. On one hand tropical and subtropical waters are usually too poor in phytoplankton to give a substantial growth of the bivalves, and on the other hand the more eutrophic temperate waters have temperatures too low for bivalve growth for often as long as half a year.

An intensive nursery-system in a temperate climate, that aims at having the bulk of its production ready for spring sales, has to make the choice of either to grow the spat in autumn when phytoplankton is present in adequate densities in the natural sea-water, and then store the graded spat during the winter at low temperatures, or to grow the spat during the winter and to add an additional amount of food, usually consisting of cultured microscopic algae, to the culturing water.

It is clear that in the latter systems, the same increase in shell length and live weight of the spat must be achieved in a much shorter period than in the natural environment (i.e. three months versus seven-eight months) and this for economic reasons.

In order to estimate the growth performances that one can expect in such a controlled nursery system, an extensive literature survey was made regarding the growth rates of spat of different commercial bivalves in various culturing devices and at various temperatures.

Since no standard procedure has been used in the studies, the original data have been transformed in various ways to give comparable information for each locality. Data from 64 papers on six species were examined : i.e. *Ostrea edulis*, *Crassostrea gigas*, *Venerupis semidecussata*, *Mercenaria mercenaria*, *Crassostrea virginica* and *Argopecten irradians*.

The growth rate is expressed as the instantaneous growth rate for 30 days (Ricker, 1968; Spencer and Gough, 1978),

$$G_{30} = \frac{30}{t} \ln \frac{W_t}{W_0}$$

where G_{30} is the instantaneous growth rate for 30 days, W_0 the initial live weight, dry meat weight or shell length, W_t the final live weight, dry meat weight or shell length, $t = t - t_0$ the time.

For a sample the value for G_{30} is usually higher when considering the increase in live weight instead of the increase in shell length. The G_{30} values are strongly affected by temperature and for G_{30} (live weight) also by the initial weight of the spat. The duration of the experiment affects the G_{30} values as well, and since the scope of this article is the growth of the bivalves during the nursery phase, data regarding experimental periods longer than 150 days have been omitted, as well as data concerning the growth of bivalve spat smaller than 1.5 mm and juveniles larger than 20 mm .

4.1.– *Ostrea edulis*.

The G_{30} values for shell length and live weight were derived from nine papers, and are given in figs 3 and 4 (Walne, 1974; Barry, 1975; Sunderlin et al., 1976; Le Borgne et al., 1978; Gimazane and Medhioub, 1979a; Moerman, 1979; Drinkwaard, 1981; Guerrero et al., 1981).

The values for shell length are maximal (i.e. almost = 1.0) at the highest temperature taken into consideration, namely 25.5 °C (fig. 3). From the G_{30} values for live weight (fig. 4) it appears, however, that the instantaneous growth rate is maximal at 20°C. At 10°C the *Ostrea edulis* spat completely ceases to grow. The influence of the initial size of the spat on the G_{30} value is important especially at 20°C. For example the G_{30} value at 10 mg equals 2.90 , whereas at 100 mg it is only 1.30 .

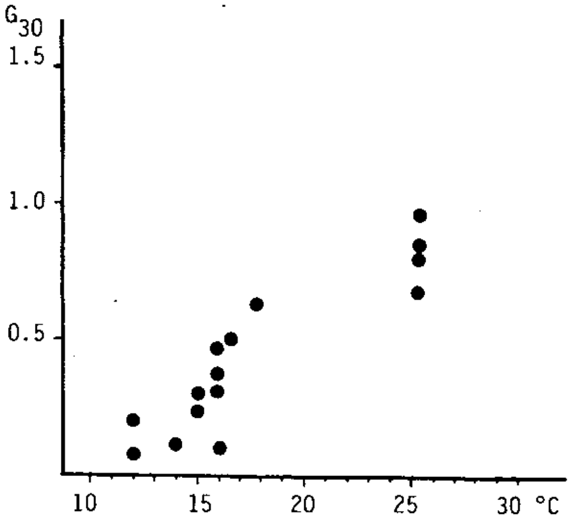

fig. 3.

Instantaneous growth rate for 30 days (G_{30}) for the shell length of *Ostrea edulis* in function of the temperature

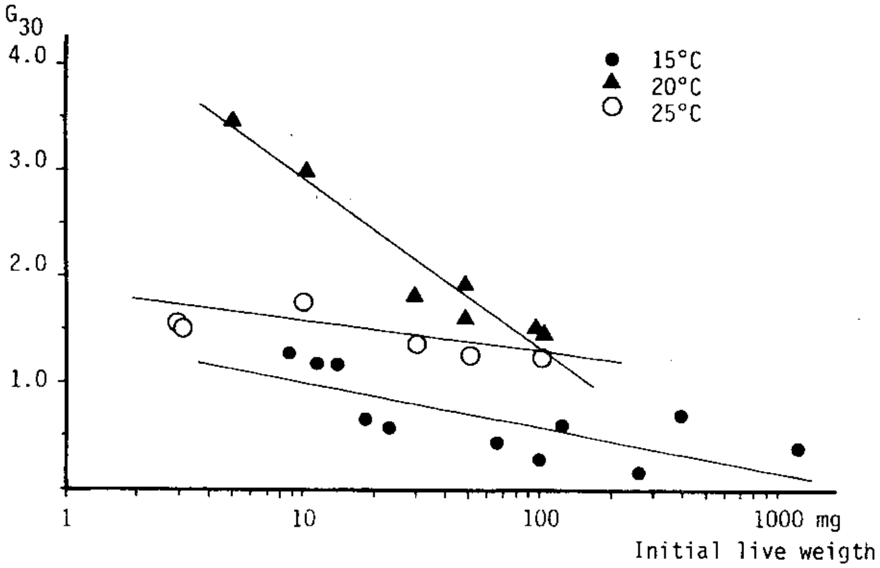

fig. 4.

Instantaneous growth rate for 30 days (G_{30}) for individual live weight of *Ostrea edulis* in function of the initial live weight

4.2.– *Crassostrea gigas.*

The G_{30} values for shell length and live weight were derived from 12 papers and are given in figs 5 and 6 (Cooke et al., 1975; Mann and Ryther, 1977; Askew, 1978; Le Borgne et al., 1978; Ley, 1978; Malouf and Breese, 1978; Spencer and Gough, 1978; Yelf, 1978; Gimazane and Medhioub, 1979b; O'brien, 1979; Breber, 1981; Spencer and Hepper, 1981).

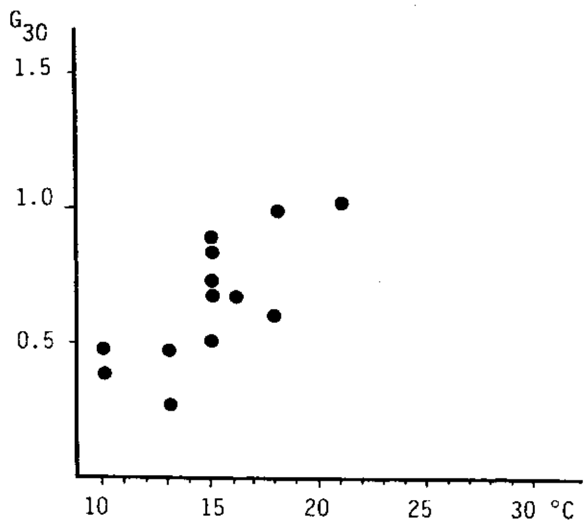

fig. 5.

Instantaneous growth rate for 30 days (G_{30}) for the shell length of *Crassostrea gigas* in function of the temperature

The G_{30} values for length are maximal (i.e. 1.0) at the highest temperature taken into consideration, namely 21°C (fig. 5). Since *Crassostrea gigas* is a subtropical species, it may be expected that even higher values may be encountered at higher temperatures. At a temperature of only 10°C there is still a substantial growth of the shell ($G_{30} > 0.30$). As for *Ostrea edulis* the influence of the initial live weight of the spat strongly affects the G_{30} values (fig. 6). At 20°C a specimen of 10 mg has an instantaneous growth rate of 4.00 , whereas a specimen of 100 mg has a G_{30} value of only 2.00 . Generally, *Crassostrea gigas* grows faster than *Ostrea edulis* under the same circumstances.

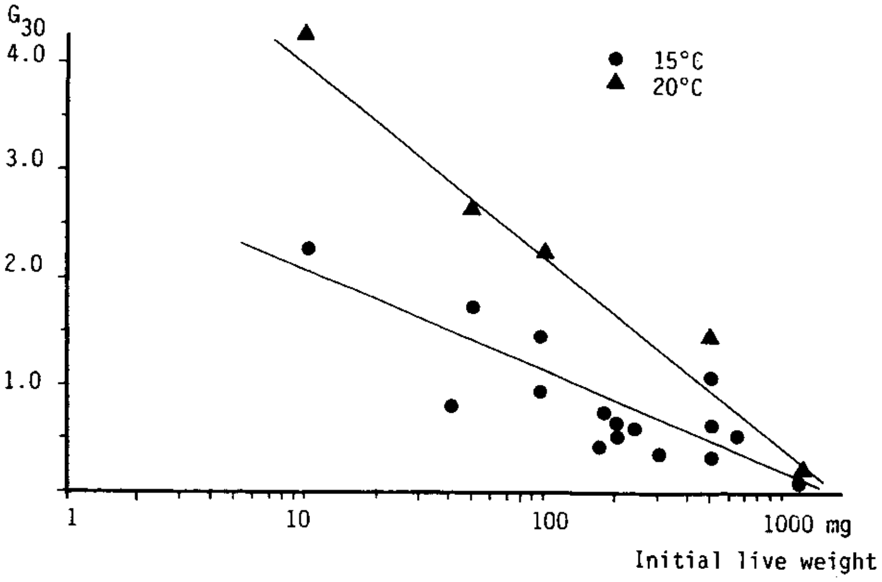

fig. 6.

Instantaneous growth rate for 30 days (G_{30}) for individual live weight of *Crassostrea gigas* in function of the initial live weight

4.3.– *Venerupis semidecussata.*

The G_{30} values for shell length and live weight were derived from 11 papers and are given in figs 7 and 8 (Lucas, 1976, 1977; Rodde et al., 1976; Le Borgne et al., 1978; Dreno, 1979; Gimazane and Medhioub, 1979c; Moerman, 1979; Claus et al., 1981; Guerrero et al., 1981; Riva and Lelong, 1981; Spencer and Hepper, 1981).

The G_{30} values for shell length (fig. 7) are more or less constant from 10 to 20°C (approximately 0.25). A maximal value of 0.75 is observed at a mean temperature of 25.5 °C. Contrary to the trend in the growth rate of both previous species, the G_{30} for live weight is apparently unaffected by the initial live weight of the spat (fig. 8). The G_{30} equals 0.45 for the range from 5 mg to 1 g. The Japanese little-neck clam is a slow grower as compared to the two oyster species.

4.4.– *Mercenaria mercenaria.*

The G_{30} values for shell length and live weight were derived from five papers and are given in fig. 9 (Walne, 1970a; Hartman et al., 1973; Sunderlin et al., 1975; Roels et al., 1976; Epifanio, 1979).

From this limited number of data it appears that the instantaneous growth rate of 3 mm spat is optimal at a temperature of 20°C. This corroborates the data given by Ansell (1968) for specimens of 4 cm (fig. 10). The hard clam grows faster than *Venerupis semidecussata* but more slowly than the oysters.

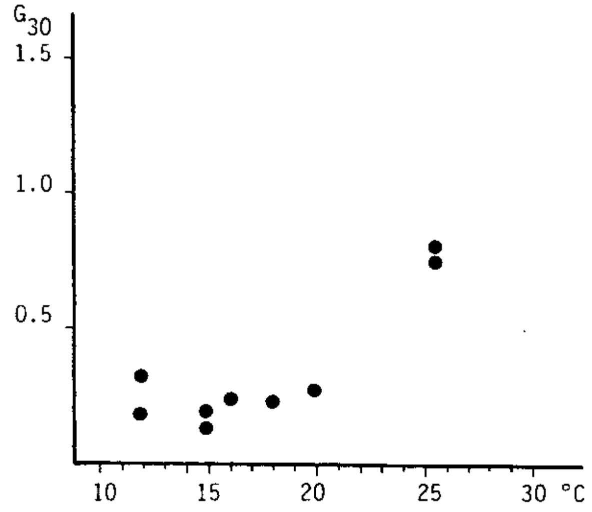

fig. 7.

Instantaneous growth rate for 30 days (G_{30}) for the shell length of *Venerupis semidecussata* in function of the temperature

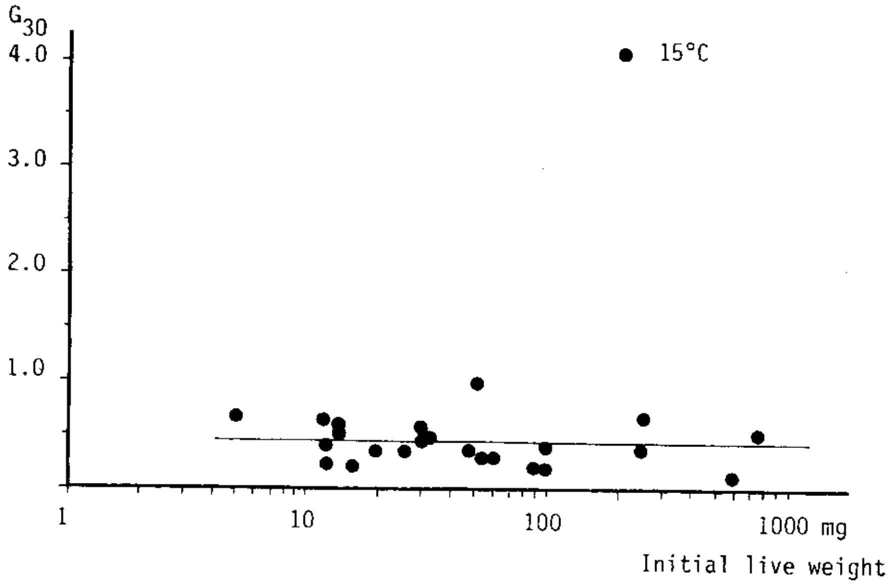

fig. 8.

Instantaneous growth rate for 30 days (G_{30}) for individual live weight of *Venerupis semidecussata* in function of the initial live weight

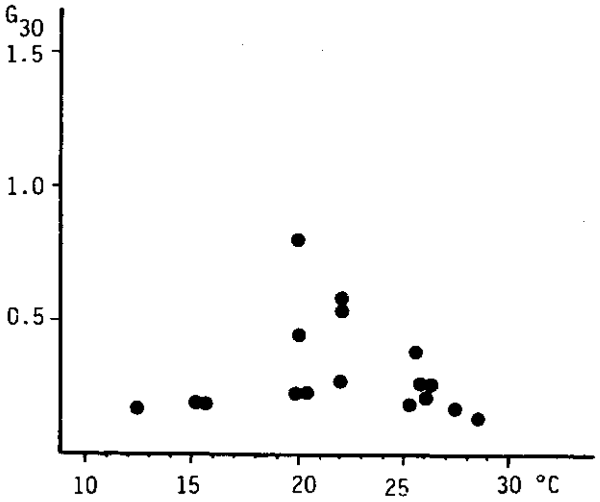

fig. 9.

Instantaneous growth rate for 30 days (G_{30}) for the shell length of *Mercenaria mercenaria* in function of the temperature

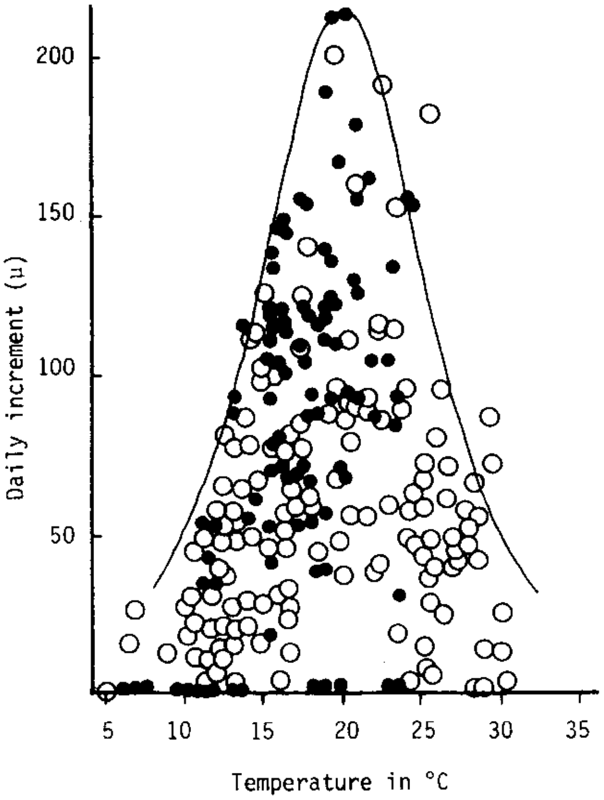

fig. 10.

The general relationship between the rate of shell growth (μ) of *Mercenaria mercenaria* based on field measurements and temperatures
(●) Sites in England; (○) North American sites

4.5.– *Argopecten irradians.*

Data from only three papers were retained. At temperatures ranging from 22-29°C, a maximal G_{30} for shell length of 0.46 has been recorded for 2 mm spat (Roels et al., 1976). Rhodes et al. (1981), however, found G_{30} values of 1.97 to 1.54 at 20°C for specimens of 2 to 4 mm. Larger specimens of 4-5 g have G_{30} values for live weight at 12 and 25°C of respectively 0.21 and 0.81 (Mann and Taylor, 1981). Since the nursery culturing of scallops is a fairly new practice, additional data are needed to draw meaningful conclusions.

4.6.– *Crassostrea virginica.*

Growth rate data of *Crassostrea virginica* in nursery operations are very scarce. From the information reported by Pruder et al. (1976) a G_{30} for shell length of 0.61 was calculated for 4 mm spat at 24°C. Based upon the figures given by Singh and Zouros (1978) a G_{30} for live weight of 0.97 for spat of 870 mg at 18°C could be derived. These very few data, however, compare very well with the figures for *Crassostrea gigas*.

It is interesting to consider these results in relation to commercial practice.

From the data shown in figs 3 through 9, one can derive the average growth rate of spat in the nursery system under various temperatures, assuming an unlimited food supply. This average growth rate is expressed as the mean time necessary to achieve the size at which the spat is ready to leave the nursery. These values have been arbitrarily set at 15 mm and 250 mg for *Ostrea edulis* and *Crassostrea gigas*, at 10 mm and 250 mg for *Venerupis semidecussata*, and at 10 mm for *Mercenaria mercenaria*. The results are summarized in table 1.

In a commercial operation, the turnover of the spat in the culturing devices, is one of the major factors determining the yearly benefits. The duration of the nursery phase is different for each species and strongly influenced by the temperature of the culturing water (Table 1). The nursery periods are very similar when calculated on a length basis and on a live weight basis. At a temperature of 15°C it takes *Crassostrea gigas* nearly ten weeks to complete the nursery stage, *Ostrea edulis* four to five months, and both clams more than six months. At 20°C *Crassostrea gigas* needs only six weeks, *Ostrea edulis* and *Mercenaria mercenaria* two months, and *Venerupis semidecussata* four months. At 25°C *Venerupis semidecussata* can achieve the final nursery stage in two months. It should, however, be pointed out that the daily food rations of the bivalves at these high temperatures are substantial. In most cases the production of these large quantities of live food is not economically feasible (De Pauw, 1981).

5.– Temperature.

The effect of temperature on the growth of bivalve spat has been studied by several authors (Mann and Ryther, 1977; Malouf and Breese, 1978; Mann, 1979a,b; Claus et al., 1981). The optimal temperature for growth usually ranges from 20 to 25°C depending upon the species. It has, however, been shown by Lough (1975) that in a mariculture installation, sustained high temperatures at which a maximal growth response is obtained, may put an abnormal stress on the animals which can result in high mortality.

An organism probably operates most efficiently when it finds itself in a set of environmental conditions which maximizes all its biological responses and not only growth. In this regard it should be emphasized that increasing the temperature will hasten growth but may divert energy from somatic growth to gonadal growth (Walne, 1976).

A temperature regime optimal for growth has to be a compromise between the stimulation of feeding and meat production on one hand, and minimizing excessive shell growth, production of gonadal material and potential physiological stresses associated with high temperatures, on the other hand. The exploitation of the advantages of increased temperature results in a greater vulnerability for prolonged stress. The animal indeed depends on limited stored reserves to maintain a normal metabolism rate during periods when the collected food is unadequate to support this process (Ansell and Sivadas, 1973).

Walne and Spencer (1974) demonstrated that there is little difference between growth at 14°C and 24°C when *Ostrea edulis* spat were only fed five *Tetraselmis* cells/µℓ/day. If the ration was increased to 10 cells/µℓ/day some positive influence could be seen resulting from the higher temperature. The experiments carried out on a larger scale by Mann and Ryther (1977) with spat of *Crassostrea gigas*, *Crassostrea virginica*, *Ostrea edulis*, *Tapes japonica*, *Mercenaria mercenaria* and *Mytilus edulis* corroborate these findings. At 15°C consistant higher values for live weight, dry meat weight, and condition index were recorded throughout the study as compared to 20°C. In our experiments the minimal food level to sustain growth at 15°C and higher, is considered to be 10 µg/ℓ of chlorophyll α (Claus et al., 1981), which was also found by Rhodes (1978, personal communication) and Rhodes et al. (1981).

From an economic viewpoint the artificial heating of large volumes of sea-water needed for commercial mollusc production is theoretically prohibitively expensive. A solution to this problem can, however, be found in the use of the waste heat of a power plant.

Some scientists advocate the direct use of marine cooling water as a culturing medium for molluscs (Malouf and Breese, 1978; Malouf, 1981). Because of the various problems inherent to a direct utilization it seems, however, that indirect use of thermal effluents (of all kinds) in a shellfish nursery system might be far more interesting (Claus et al., 1981).

Table 1

Mean time (days) necessary to achieve the nursery cycle
for *Crassostrea gigas*, *Ostrea edulis*, *Venerupis semidecussata* and *Mercenaria mercenaria*
at different temperatures

Species	Temperature (°C)	Initial		Final		Time for length (days)	Time for live weight (days)
		Length (mm)	Live weight (mg)	Length (mm)	Live weight (mg)		
C. gigas	12	3	10	15	250	127	
	15					69	68
	18					55	
	20					48	36
O. edulis	12	3	10	15	250	402	
	15					172	136
	18					82	
	20					64	59
	25					58	70
V. semidecussata	12	3	15	10	250	201	
	15					190	188
	18					157	
	20					134	
	25					52	
M. mercenaria	12	3	15	10	250	212	
	15					201	
	18					144	
	20					52	
	25					103	

6.– Stocking density and water flow.

The growth of small cultchless spat in a nursery system is very sensitive to the stocking density and water flow. Whatever growing system is chosen, its mean feature must be a virtually unlimited supply of new water reaching every individual animal. In the monolayer practices such as trays, a rule of thumb for stocking density is that "the juveniles may touch but not overlap" (Maskell, 1973).

In most commercial operations working in the natural environment, however, much lower stocking densities are applied (0.2 g/cm^2). Although this may seem a waste of equipment space, one can consider it worthwhile in saving labor for thinning operations (Ley, 1978). Regular servicing remains, however, an absolute necessity. It is the experience of most growers that thorough cleaning of the stock and the meshes is essential if satisfactory survival and growth rates are to be achieved with small spat (George, 1975). In the natural environment it is also important to avoid the spat to bunch in the trays. This is usually accomplished by maintaining the support surfaces as flat and horizontally as possible.

In the onshore nurseries these problems are overcome by using trays and trenches, and subsequently increasing the stocking densities. Present work at Conwy, UK, indicates that good growth and survival of small oysters is obtained up to a final stocking density of 1 g live weight/cm^2 of tray (Spencer and Gough, 1978). This corresponds with 200 000 specimens of 50 mg/m^2. This is ten times more than the density recommended earlier by Walne and Spencer (1971) and Walne (1974) for their recirculating system; ten times more than the stocking densities applied in the subtropical nursery at St Croix (Rodde et al., 1976), and four times more than the density recommended by Lucas (1977) for the raceways with lantern nets.

The great breakthrough in technology that allowed to increase the stocking density substantially, is the upflow system as described in a previous chapter. In these upwelling systems with pumped sea-water, stocking densities of 20 g/cm^2 and more can be achieved (Le Borgne, 1981; Williams, 1981). The application of this technique making use of the tidal action (Spencer and Hepper, 1981) resulted in a compact system with a maximum capacity of 3 to 6 g/cm^2. For the gravity-fed nursery plant MARIOS in the Netherlands, the recommended stocking density, however, is only 0.5 g/cm^2 (Drinkwaard, 1981).

There is much diversity in the data on the flow rate of the water in nursery systems. A suitable water current is required to stimulate feeding and carry away faeces. From the very basic research of Walne (1972) on the influence of current speed, body size, and water temperature on the filtration rate of *Ostrea edulis*, *Crassostrea gigas*, *Mytilus edulis*, *Venus decussata* and *Mercenaria mercenaria*, it appeared that there was a significant correlation between the flow rate and the filtration rate. It was stated that the large volumes of water pumped by the bivalves are primarily for feeding rather than for respiration. At some point the animal reaches its maximal filtering rate, and increasing the water flow rate will have no further effect (Wilson, 1980). In an earlier study, Wilson and La Touche (1978), however, found that there is no evidence that current velocity alters ingestion rates of bivalves. Neither change in direction of flow, nor variation in magnitude caused a detectable variation in the pattern of intracellular digestion.

Very few studies have directly linked filtration and growth (Kirby-Smith, 1972; Walne, 1972). It was assumed by the first author that the limiting factor for growth was the concentration of suspended food present in the water, more than the flow rate itself.

Recently, a very interesting study has been made by Rodhouse and O'Kelly (1981) on the flow requirements of *Ostrea edulis* and *Crassostrea gigas* in an upwelling column. Since the stocking density of spat in this type of culturing device is very high, the flow rates become very critical. Flow rates below the optimum cause a reduction in growth rate, while flow rates above the optimum result in an unnecessary increase in the cost of pumping and heating of the water and of producing algal cultures necessary to feed the spat.

Flow requirements were assessed by determining the rate of clearance of the suspended algal cells by a population of oysters. This clearance rate is the equivalent of the filtration rate of an individual oyster as calculated by Bayne (1971) and Hildreth and Crisp (1976). A maximal clearance rate is obtained at a certain flow rate. At this maximal clearance rate no effect of food concentration on this rate was observed. Temperature and body size, on the contrary, definitely affect the clearance rate. The whole study resulted in two equations which can be used to predict the flow requirements for 90 % clearance between 10 and 20°C :

$$FR = (0.47 + 0.04\ T)\ LW^{-0.26} \qquad \text{for } \textit{Ostrea edulis}$$

$$FR = (-\ 0.92 + 0.17\ T)\ LW^{-0.32} \qquad \text{for } \textit{Crassostrea gigas}$$

where FR is the flow requirement for 90 % clearance expressed in mℓ/min/g, T the temperature in °C and LW the individual live weight in g.

Inversely these equations can be used to calculate the maximal stocking capacity of an upwelling tube at a given flow rate and temperature. In table 2, the maximal number of *Ostrea edulis* and *Crassostrea gigas* spat at various sizes are given for the nursery plant in Ostend. Maximum stocking density varies between 10 to 45 g/cm^2. It should, however, be pointed out that a clearance rate of 90 % is very favorable from the economical point of view, but the experience has shown that the growth rate of different species (especially *Venerupis semidecussata*) is decreased at such high clearance rates. Kirby-Smith (1972) suggested that the growth rate of the scallop *Argopecten irradians* begins to decline when the concentration of chlorophyll α drops below 60 % of the inflow and that growth ceases completely when the concentration drops below 30 % .

Table 2

Stocking capacity of nursery pilot plant at the Institute for Marine Scientific Research (IZWO)
Temperature : 15°C; flow rate of heated sea-water : 60 000 mℓ/min;
number of upflow cylinders : 16; diameter of one upflow cylinder : 33 cm;
surface of one upflow cylinder : 855 cm^2

Live weight (g)	Flow requirement (Rodhouse and O'Kelly, 1981) (mℓ/min/g)	Maximal total weight (g)	Maximal total number of individuals	Maximal number of individuals per cylinder	Maximal stocking density (g/cm^2)
Ostrea edulis					
0.010	3.54	16 934	1 693 432	105 840	19.80
0.050	2.33	25 751	515 000	32 000	30.11
0.100	1.95	30 769	308 000	19 230	35.97
0.250	1.53	39 000	156 000	9 800	45.60
Crassostrea gigas					
0.010	7.11	8 439	843 265	52 704	9.87
0.050	4.25	14 113	282 270	17 642	16.50
0.100	3.41	17 618	176 182	11 011	20.60
0.250	2.54	23 621	94 485	5 905	27.62

As a rule of thumb Bayes (1979) uses the ratio :

1 m^3 water/min/ton of seed.

For a temperature of 6°C this corresponds to the flow rate proposed by Drinkwaard (1981) at a temperature x :

x m^3/h/100 kg .

The latter formula corroborates the equations of Rodhouse and O'Kelly (1981).

7.– Feeding regime.

Knowledge of feeding and biodeposition rates at different food concentrations and under different circumstances is important to optimize the nursery.

Various investigations have been performed to establish the food value of different algal species for bivalve spat. Reviews are given by Walne (1970a), Epifanio (1976) and De Pauw (1981). These studies provide valuable information, but often the experimental conditions are so specialized that extrapolation of these results to a larger scale is very difficult if ever possible, and any comparison as to the effects of mixed populations in the natural environment are very difficult to make. Even the laboratory studies with mixed diets which usually result in higher growth rates and lower mortality rates of the bivalves than the single foods (Hartman et al., 1973; Epifanio and Mootz, 1976; Epifanio, 1979; Ewart and Epifanio, 1981), are hard to extrapolate to pilot- or commercial-scale operations mainly because some algal species are very difficult to keep in large-volume cultures.

On a large scale *Skeletonema costatum, Phaeodactylum tricornutum, Tetraselmis suecica* and *Monochrysis lutheri* have been used successfully in temperate climates (Lucas, 1977; Mann and Ryther, 1977; Mann, 1979a,b). In subtropical conditions *Bellerochia spinifera, Chaetoceros simplex, Thalassiosira pseudonana* and *Isochrysis galbana* Tahiti strain have been used with success (Sunderlin et al., 1975; Rodde et al., 1976).

Efficient production of bivalves in controlled environments requires the definition of an adequate daily ration. Although considerable information exists concerning the filtration rates of bivalves, there is little concensus regarding rates of ingestion and selection of particles (Epifanio and Ewart, 1977).

A very clear relationship exists between the food concentration, the size of the particles, and the filter-feeding behavior of the bivalves. Particles are retained effectively by most bivalve species down to 3 µm in diameter (Owen, 1974; Winter, 1978). Particles of 1 µm are retained less efficiently but when considered in terms of total volume rather than in terms of efficiency, similar quantities of these small particles are removed by the bivalves than of the larger fractions (Haven and

Morales-Alamo, 1970). Particles greater than 55 µm are ejected for 90 % by small *Mytilus edulis* of 1.5 cm (Gabbott et al., 1976).

Generally, it has been assumed that bivalves have the ability to select particles for ingestion, based on the shape, the size, and the weight of the particles (Ali, 1970; Wilson, 1980). With regard to a selection based on chemoreception there is no consensus among the authors. Dwivedy (1973) gave evidence for the presence of chemoreceptors in the labial palps and suggested a chemical selection of the ingested particles. The results of the studies by Winter (1972) and Foster-Smith (1975a), however, are in contradiction with the hypothesis.

Various authors have shown that bivalves control the rate of phytoplankton intake in relation to the algal cell-concentration in the culturing medium (Ali, 1970; Winter, 1970, 1973; Tenore and Dunstan, 1973a,b; Foster-Smith, 1975a,b; Schulte, 1975; Langton and McKay, 1976; Epifanio and Ewart, 1977; Epifanio and Roels, 1977).

The quantity of phytoplankton consumed increases in proportion to the algal cell-density, reaching a plateau where it is constant, independently of the particle-concentration, while on the other hand the filtering rate decreases. Finally, the ingestion rate decreases again with further increasing particle concentrations. This occurs when the production of pseudofaeces starts (Winter, 1978).

The concentration which is just below the threshold of pseudofaeces production, the "pseudofaeces-free cell density" is very close to the optimal food concentration since at that level the minimal energy must be put into filtration activity by the animal and yet all the filtered cells are ingested.

The regulation of the filtration rate is not only influenced by cell density but is also a function of algal size. The relation between the cell volume and the most favorable density of algal food for spat of *Ostrea edulis* and *Mercenaria mercenaria* has been established by Walne (1970). For example, the optimal cell concentration of a medium-sized algal species of 100 μm^3 (± 6 µm in diameter) is ± 20 cells/µℓ for *Ostrea edulis* and ± 25 cells/µℓ for *Mercenaria mercenaria*. Generally, the optimal cell densities given by Walne (1970a) are slightly lower than the "pseudofaeces-free cell density" given by different authors for the given algal species (Foster-Smith, 1975a; Schulte, 1975; Epifanio and Ewart, 1977).

An estimation of the optimal cell density can also be made based on the knowledge of the energy budget of the oyster spat. The daily ration of a juvenile oyster of 10 mg live weight is estimated at 20 % of its dry meat weight [200 µg] (Walne and Spencer, 1974; Epifanio and Ewart, 1977). These 40 µg of dry algal material correspond on the average with 2 million medium-sized phytoplankton cells per oyster of 10 mg, or 10^8 cells/g live weight. Starting from a calculated flow requirement of 4 mℓ/min/g live weight for an oyster of this size (Rodhouse and O'Kelly, 1981), the cell concentration of the flowing suspension is thus approximately 35 cells/µℓ which corresponds with the mean optimal concentration given by Walne (1970a).

Langton and McKay (1976) have shown that discontinuous feeding using a 6 h feeding – 6 h unfed periodicity, maximized the growth of *Crassostrea gigas* spat when compared to continuous feeding. A digestive rhythm that determined the assimilation efficiency was suggested. Analogous experiments by Winter and Langton (1976) with *Mytilus edulis*, however, dit not corroborate these findings. Wilson and La Touche (1978) gave evidence that the cyclic feeding-pattern of *Ostrea edulis* is not endogenous but depends on the food availability. With respect to aquaculture this would imply that the spat should be maintained at a constant optimal food level.

8.– Economics.

Presently it is impossible to draw firm conclusions with regard to the future of mollusc nurseries. All systems presented in this paper have proven to be biologically feasible but the economics should be evaluated. The type of technology which shall be selected depends largely on the geographical location of the nursery. Indeed, different places may be characterized by different climatic and ecological conditions and divergent costs for land, energy, labor, water treatment, food production, purchase and transport of seed, taxes, etc.

Regardless of the system used, the market price of the produced spat is more or less constant, contrary to the price of natural seed which varies as much as 1:4 according to the amount of seed captured and collected. Currently, 100 million artificially-bred *Crassostrea gigas* spat are sold annually in France and the UK combined (Lintell, 1980). These countries are indeed the two major producers in Europe.

Directive prices of nursery spat from French and British firms are given in table 3.

Table 3

Price per 1000 in £ and in FF (converted to US $) of nursery reared spat

Size (mm)	*C. gigas*			*O. edulis*			*V. semidecussata*		
	£	FF	$	£	FF	$	£	FF	$
3-4	5.70		9.73	6.00		10.24	5.70		9.73
6	7.40		12.63	7.70		13.15	7.40		12.63
8	8.50	66	14.51	8.80	75	15.02	8.50	70	14.51
10	9.70	78	16.56	11.00	85	18.78	9.70	88	16.56
12-15	12.50	95	21.34	14.50	95	24.76	12.50	100	21.34
15-20	14.80		25.27	17.80		30.39	14.80		25.27
20-25	18.00		30.73	22.50		38.41	18.00		30.73
25-30	21.50		36.71	27.50		46.95	21.50		36.71

An estimation of the cost structure of a European nursery operation working in the natural environment was given by George (1975) :

Purchase of seed	46.5 %
Equipment (written off over 5 years)	4.5 %
Labor	22.5 %
Overheads (100 % of labor)	22.5 %
Operating costs	2.0 %
Insurance	2.0 %

Another estimation for an extensive operation has been made by Walker and Gates (1981) :

Seed stock purchase	16.7 %
Total maintenance + repair and replacement of equipment	19.9 %
Labor (inclusive social security payments)	58.0 %
Miscellaneous	9.3 %
Taxes	2.2 %
Insurance	9.0 %

The major costs are labor expenses and seed-stock purchase. Since under natural conditions a 50 % mortality is not unusual, the costs to purchase the spat are relatively high.

In the more complicated onshore operations investment costs, energy costs, and eventually costs to produce phytoplankton may become substantial as well. The advantages of these systems must be derived principally from the lower mortality rates (5 - 25 %), the higher stocking capacity and the higher growth rates.

The increase in value of the spat after the nursery stage is very small :

O. edulis	3 → 15 mm	US $	14.50/1000 = 1.5 cents/piece
C. gigas	3 → 15 mm	US $	11.60/1000 = 1.2 cents/piece
V. semidecussata	3 → 10 mm	US $	6.83/1000 = 0.7 cents/piece

If one compares these figures with the pumping costs as estimated by Drinkwaard (1981), namely 0.37 cents/spat estimated by Spencer and Gough (1978) for an experimental period of four weeks, taking the costs for algal food, namely 2 cents/spat for monospecific cultures into account (Walne, 1970b; Malouf and Breese, 1978), as well as 0.2 cents/spat for induced blooms (De Pauw, 1981), it is clear that setting up a nursery aquaculture-system, independently from a hatchery or an ongrowers operation, is not always an attractive investment.

Without a better understanding of the nutritional requirements of bivalve spat associated with the technological development of an optimized system, and next to that the development of an inexpensive artificial food, the economic feasibility of intensive nursery culturing must remain in doubt. To set up a nursery of a particular type, a reasonable compromise should be worked out, between the costs cited above and the corresponding biological responses of the bivalves that may be expected and which determine the total production in the system. For example, seasonally operated systems with unheated water, might be more

Table 4

Synopsis of the replies to the inquiry made by Persoone and Claus (1979) in the framework of the COST 46 program

Location	Country (*)	Type (**)	Spat cultured in the natural environment			Onshore culturing		Controlled food production			Inert foods	
			Bottom culture	Off-bottom		Pumping from		Natural phyto-plankton blooming		Monospecific cultures	Supplement	Substi
				Trays trestle	Trays raft	Open sea	Enclosures	Outdoors	Indoors			
Ostrea edulis												
Ostend	B	E			+		+	+			+	+
Nykøbing Mors	DK	C	+			+		+				
Barfleur	F	C				+	+			+		
Caen	F	E	+			+				+		
Ile de Ré	F	C				+	+	+				
Sète	F	E			+	+						
Chioggia	I	E		+	+							
Taranto	I	E		+		+		+				
Abbotstown	IR	E	+	+	+							
Carna	IR	E	+	+	+	+	+	+		+		+
Carna	IR	C			+	+		+		+		
Coleraine	IR	E	+	+	+							
Connemara	IR	C	+	+								
Derryherbest	IR	C	+		+							
Rossmore	IR	C	+	+		+	+	+				
Fort San Lucian	M	E	+	+	+							
La Coruña	S	E			+							
Villegarcia de Arosa	S	E			+			+		+		
Fawley, Southampton	UK	C		+								
Herts	UK	C			+							
Isle of Anglesey	UK	C	+	+		+	+	+		+		
Isle of Lewis	UK	C			+	+						
Guernsey, Channel Isl.	UK	C	+	+	+	+		+				
Totnes, Devon	UK	C		+								
West Mersea, Essex	UK	C	+	+	+	+						
Whitstable	UK	C					+					
Portoroz	Y	E			+							
Rovinj	Y	E			+							
Crassostrea gigas												
Ostend	B	E			+		+	+			+	+
Barfleur	F	C				+	+			+		
Brest	F	E	+		+			+	+	+		
Caen	F	E	+		+							
Ile de Ré	F	C				+	+	+				
Sète	F	E				+						
Langballigau	G	E		+	+	+		+	+	+		
Trieste	I	E			+							
Carna	IR	C			+	+		+	+			
Carna	IR	E	+	+	+	+	+	+		+		
Coleraine	IR	E	+	+	+							