Shellfish culture development and management
-
Développement et aménagement de la conchyliculture

International Seminar In La Rochelle (France), March 4-9, 1985
Séminaire International de La Rochelle (France), 4-9 mars 1985

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GROWTH
EMPLOYMENT

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on Technology, Growth and Employment
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Le Séminaire International

sur

LA RECHERCHE EN SOUTIEN
DU DEVELOPPEMENT ET DE L'AMENAGEMENT
DE LA CONCHYLICULTURE

s'est tenu à La Rochelle (France)
du 4 au 9 mars 1985

sous l'égide
du
Groupe de Travail
TECHNOLOGIE, CROISSANCE, EMPLOI
constitué par décision des Chefs d'Etat et de Gouvernement
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Objectives

The Molluscan Shellfish Culture Seminar was organized at the initiative of the Planning Group on Aquaculture that came out, following Canadian proposal, from the Working Group "Technology, Growth and Employment" established by the Heads of States and Governments at the Versailles Summit (June 1982).

The terms of reference of this Planning Group on Aquaculture are, briefly :

- "to document the present production and research and development programmes in member countries (Canada, Federal Republic of Germany, France, Italy, Japan, UK, USA and EEC) and estimate future economic trends,

- to review and analyse trends that lead to changes in the scientific, technological, economic and legal elements related to aquaculture,

- to stimulate thinking on the research and development resources required,

- to strengthen existing collaborative efforts among member countries and foster initiation of new ones where appropriate,

- to provide a continuing forum to consider the contribution that science and technology can make to aquaculture, and to economic growth and employment opportunities."

JUSTIFICATION AND OBJECTIVES OF THE SEMINAR

With an overall world output of about 3,2 millions tons, bivalve mollusc culture stands well ahead of all animal mariculture. The success of mollusc cultivation, especially of such sedentary species as oysters and mussels, is due to the advantages offered by a combination of specific features of their biology and ecology which are of strategic significance for expanding mariculture in coastal waters, notably :

- the facility to collect natural spat and, thus, to artificially enhance recruitment of wild stocks,

- their filter feeding nature which permits high cultivation densities in open waters and the use of a part of marine productivity so far unutilized,

- their sedentary nature, which eliminates the need for retention structures, facilitates the extention of cultivation into open waters and enables them to stand wide ranges of envivonmental variations,

- at the same time, the most critical issue in fisheries management of regulation access to the ressource is substantially eased through the allocation of sites.

These biological features have played a major role in the expansion of bivalve molluscan culture in various countries, both developed and developing.In additions, being little capital intensive, it generates a proportionally high number of jobs. It still offers large opportunities for expension, especially in contries where coastal waters are not yet intensively used. It was on this background considerations that the Planning Group on Aquaculture selected shellfish culture as a priority topic for its assessment of prospects and conditions of aquaculture development.

However, the above listed strengthes are offset by specific weaknesses, which become acute as culture and use of coastal waters intensify. These are :

- the vulnerability of larvae (detrimental to spat collection) and adults (resulting in decline in growing performances, higher mortalities and insalubrity), in relation their filtering and sedentary features and the degradation of water quality and carrying capacity of coastal ecosystems,

- the difficulties of therapeutical treatments and protection against diseases in a fluid environment,

- the competition amongst farmers for a naturally limited carrying capacity, resulting of high levels of development into overstocking and, then, reduction of growing performances and higher susceptibility to mortalities and diseases,

- the competition with other uses of littoral environments (industry, urbanization, tourism, agriculture, fishing) which tends to reduce the area and, under certain conditions, the carrying capacity available in highly demanded geographical sectors.

ORGANIZATION OF THE SEMINAR

When preparing the Seminar, the following objectives were selected :

- to identify the need and opportunities offered by research and technological progress for the development of bivalve molluscan cultivation,

- to assess their likely economic effects as well as their probability of success,

- to determine priorities for research and technological development and the actions liable to benefit from international cooperation.

The Seminar was held in La Rochelle (France) from 4 th to 9 th March 1985. It was attended by 53 scientists from 7 countries (the list of participants is given in Appendix 1). The discussions were divided in three parts :

- an introduction during which the national achievements on bivalve molluscs culture of social and economic importance as well as the contraints and the perspectives of development were reviewed and assessed,

- five major topics of research and technological development, namely pathology, genetics, technology and biotechnology, management of molluscan shellfish stocks and their ecosystems, management of exploitations ; for each of them, the present state of the art and priorities were presented and analysed ;

- a conclusion containing recommendations regarding priorities for action and opportunities for international cooperation ; these recommendations were drafted to be addressed to national fisheries administrations and industry ; they are presented in the conclusions.

Objectifs

Le Séminaire sur la Conchyliculture a été organisé à l'initiative du Groupe de Planification sur l'Aquaculture qui est issu, sur une proposition du Canada, du Groupe de Travail "Technologie, Croissance et Emploi", établi par les Chefs d'Etât et de Gouvernement lors du Sommet de Versailles (Juin 1982).

Les termes de réfèrence du Groupe de Planification sur l'Aquaculture sont, en bref :

- "de faire l'état de la production, et des programmes de recherche et développement des pays membres (Canada, Etats-Unis d'Amérique, France, Grande-Bretagne, Italie, République Fédérale d'Allemagne, Japon et d'évaluer les tendances économiques futures,

- de faire la liste et d'analyser les tendances qui amènent les changements dans les composantes scientifiques, technologiques, économiques et législatives de l'aquaculture,

- de stimuler la réflexion sur les besoins en recherche et développement,

- de renforcer les efforts de collaboration entre les pays membres et d'en amorcer de nouvelles, si elles sont justifiées,

- de fournir un forum permanent pour discuter les apports de la science et de la technologie à l'aquaculture, ainsi qu'à la croissance économique et la création d'emplois."

JUSTIFICATION ET OBJECTIFS DU SEMINAIRE

Avec une production globale de 3,2 millions de tonnes, la conchyliculture est de loin la première production animale en aquaculture marine. Le succés de l'élevage d'espèces sédentaires telles que l'huitre et la moule, est liée aux avantages combinés de leur biologie et de leur écologie, qui ont un rôle essentiel dans l'expansion de l'aquaculture dans les eaux côtières, notamment :

- la facilité de collecter des naissains naturels et, ainsi, d'augmenter le recrutement des stocks sauvages,

- leur alimentation par filtration, qui permet des densités élévées en élevage en mer et l'utilisation d'une partie de la production marine inutilisable autrement,

- leur nature sédentaire, qui élimine le besoin de structures de confinement, facilite le développement de l'élevage en mer, et leur aptitude à supporter de larges variations des conditions de l'environnement,

- en même temps, le point le plus critique de l'aménagement des pêches, qu'est l'allocation de la ressource, est considérablement facilité par le système des concessions.

Ces caractéristiques biologiques ont joué un rôle important dans le développement de la conchyliculture dans divers pays, développés ou en développement. De plus, nécessitant peu de capitaux, elle crée un nombre realtivement plus important d'emplois. Elle offre de grandes possibilités d'expansion, particulièrement dans les pays où les zones côtières ne sont pas encore utilisées de façon intensive. C'est avec ces considérations préliminaires que le Groupe de Planification de l'Aquaculture a choisi la conchyliculture comme sujet priotaire d'évaluation des perspectives et des conditions du développement de l'aquaculture.

Cependant les avantages énumérés plus haut sont balancés par des inconvénients particuliers, qui deviennent sensibles dès que l'utilisation de la zone côtière s'intensifie. Ce sont :

- la fragilité des larves (défavorable à la collecte de naissain) et des adultes (qui entraine des baisses de croissance, des mortalités et l'insalubrité), liée à l'alimentation par filtration et la sédentarité, la baisse de la qualité de l'eau et de la capacité trophique des écosystèmes côtiers,

- la difficulté d'effectuer des traitements thétapeutiques et de se protéger des contaminations dans un environnement liquide,

- la compétition entre éleveurs pour une production naturelle limitée, qui aboutit à un niveau élevé de surdensité et, alors, à une réduction de la croissance et une plus grande sensibilité aux maladies et mortalités,

- la compétition avec les autres utilisateurs du littoral (industries, urbanisation, tourisme, agriculture, pêche) qui tendent à réduire les zones et, dans certains cas, la capacité trophique de certains secteurs géographiques très demandés.

ORGANISATION DU SEMINAIRE

Lors de la préparation du Séminaire, les objectifs suivants ont été sélectionnés :

- identifier les besoins et les opportunités offertes par la recherche et les progrès technologiques pour le développement de la conchyliculture,

- évaluer leur impacts économiques aussi bien que leurs chances de succés,

- fixer les priorités pour la recherche et le développement technologique et les actions pouvant tirer bénéfice d'une coopération internationale.

Le Séminaire s'est tenu à La Rochelle (France) du 4 au 9 Mars 1985. 53 scientifiques de 7 pays y ont participé (leur liste est fournie en annexe). Les discussions ont été divisées en trois parties :

- une introduction au cours de laquelle, pour chaque pays, ont été passées en revue et évaluées les productions significatives de la conchyliculture ainsi que les les perspectives de développement ;

- cinq points essentiels de recherche et de développement technologique, qui sont la pathologie, la génétique, la technologie et biotechnologie, la gestion des stocks de mollusques et des écosystèmes, la gestion des entreprises ; pour chacun d'entre eux, l'état de l'art et les priorités sont présentées et analysées ;

- une conclusion qui comprend les recommandations sur les priorités d'action et les possibilités de coopération internationale ; ces recommandations ont déjà fait l'objet d'une première rédaction et ont été présentées aux administrations nationales des péches et aux secteurs de la production ; elles sont présentées dans les conclusions.

FIRST PART : NATIONAL REVIEWS
PREMIERE PARTIE : BILANS NATIONAUX

A REVIEW OF THE ECONOMIC STATUS OF MOLLUSCS - SHELLFISH CULTURE

J.P. TROADEC *

Objective : To describe the value of shellfish culture in economic and social terms and evaluate its potential for expansion by identifying and ranking the major constraints and the ways in which research and development can overcome them.

From the various reports given, it appears that the economic importance of shellfish culture differs greatly between the different member countries of the working group. The differences relate to production volumes, which vary widely between countries, and also to methods. One feature widely discussed was that the production figures often included the captured and the cultivated stocks.

In that respect, aquaculture is basically an extensive mode of exploitation which is similar to ranching on land. However the intensity of such interventions varies considerably where natural ecosystem manipulations, to improve or channel their production, are not restricted to seeding but include also removal of competitors and pestsand the provision of artificial "reefs". The example given was of scallop, the production of wild stock having being boosted from 30 000 tonnes 100 000 tonnes by intensive seeding, and elimination of starfish.

Production data

Although large quantities of molluscs are collected in the different countries, there are only few cultivated species with significant production. Table 1 summarizes the national productions for the predominant species, expressed in tonnes of whole weight.

Three species of oysters constitue the dominant productions of the countries represented in the working group : Crassostrea gigas, virginica and Ostrea edulis, the last one with high commercial value, being hit by chronic epizootics in some countries.

The production obtained by cultivation fluctuates widely, depending on the shellfish culture tradition of these countries, and the size of their national markets. For Canada, the culture of O.edulis remain at a very low level. In France, the biggest part of the production is of Pacific oyster, the other species being practically eradicated by epizootic diseases. In Germany, oyster production is barely significant, and the potantial is limited. Italy, without a national oyster market, sends its production to Northern Europe. Japan remains one of the largest producers of cultivated oysters, with an output of more than 250 000 tonnes. For the United Kingdom, oyster culture is at a low level and dependent on the presence of natural beds which are harvested for seed. Furthermore, the local market for live oysters is very small. The U.S.A. produces about 125.000 tonnes of cultivated oysters, which is one-tenth of its oyster production.

For the countries of the working-group, oyster production based on a culture cycle from spat collection to rearing and marketing, accounts for 490.000 tonnes of whole oysters. The potential for expansion could, in biological terms, be roughly of the same level. Such potential will be higher in some countries than in others. The economic aspects of such potentials will be discussed later.

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* Institut Français de Recherche pour l'Exploitation de la Mer,
Direction des Ressources Vivantes, 66 avenue d'Iéna, 75116 **Paris**, France

After oyster, mussel culture is very often the next most important shellfish culture activity. It has been developed more intensively in Europe than elsewhere, and this may reflect the location of market, i.e. that mussel production in American countries and in Japan is comparatively less developed because of market limitations. In Japan development is beginning.

Mussel culture is presently expanding in Italy and Germany, were the average annual production of around 15 000 tonnes in 1982, was doubled in 1983. The United Kingdom only produces 750 tonnes of cultivated mussels mainly because of a natural population harvest. As far as Japan is concerned, mussel production may have been inhibited because some toxicity occurred which compromised human consumption and marketing. It is worth noting that two countries, Spain and the Netherlands, which are not members of the working group, are among the world's largest mussel producers.

Pectinid culture competes with scallop fisheries and depends on natural spatfall. Man's exploitation of these species may move towards population enhancement, using hatchery-reared spats. An actual culture, with technical support and rearing systems, is only found in Japan. In that country, pectinid culture produced 72 000 tonnes in 1982, which makes it an important activity. In many other countries, culture trials are being made, either with hatchery-reared spat or by collection of natural seed. Canada, France, the United Kingdom and the U.S.A. have Research and Development programmes to develop pectinid culture.

The other species of molluscs which are cultivated are living in the sediment, most of which are grouped together as "clams". Only two species have reached a significant production level, these are Mercenaria mercenaria, 6 000 tonnes of which are produced in the United States, and the Manila clam, known under two scientific names (Ruditapes philippinarum and Venerupis semidecussata). The culture is still on a pilot scale, but 1 000 tonnes were produced in the United States and 300 tonnes in France. Generally speaking, clam culture could exhibit a strong development, due to its present high economic value, and because it constitutes an opportunity for diversifying shellfish production.

Total value of shellfish production

The total value, expressed in US $ for all member countries, is higher for the captured species (724 millions US $) ; the cultured species account for 429 million US $. This fact is mainly due to the high proportion of captured oysters in the United States, and to highly diversified catches of different species in Japan.

In three countries shellfish cultures alone account for more than 100 million US $ per year (that is USA, Japan and France), while the income for shellfish culture and harvest is very much smaller for Canada, Germany, UK and, to a lesser extent, Italy. It is worth noting that biological potential for shellfish cultivation is generally high in those countries with low current levels of production by the same ratio. Such biological potentials are very high for oysters and clams in Canada and the UK, and for mussels in France, Italy and Japan. Today, mussel culture in Japan is at a very low level.

Employment figures

It is rather difficult to give precise figures of direct employment for the shellfish culture industry because of lack of reliable statistics and of part time employment due to climatic and market variations. As an exemple, half of the French oyster production is usually sold during the last two months of the year. Therefore, in all countries and for most of the products, one has to consider a certain proportion of part-time jobs. Japanese data were given in

units of production, one unit being assessed as 2.5 people. In many countries, shellfish farming is a family business and the actual employment numbers are probaly probably under-estimated.

Accepting that a full time job corresponds to 2 part-time jobs, the total manpower for shellfish cuture corresponds to approximately 200 000 people, but such manpower is unevely distributed across the national production levels. Shellfish cultures in France and Japan are operated with large numbers of workers, whereas in the U.S.A., few shellfish cultivators are able to ensure large productions. In the smaller producer countries, which are still on a developmental stage, the ratio between production and manpower seems to be affected by size-related effects since the production units are generally smaller.

Constraints (Table 2)

Shellfish culture quite often is subjected of different constraints, which can be classified as follows :

- environmentally related constraints
- technological constraints
- economic constraints

Climatic conditions are not usually considered as constraints. Not all species can be reared in a given area, because of their ecological requirements for satisfactory growth and reproduction but the diversity of species is sufficient to quarantee a suitable organism for most sites. An exception may be found in Canadian oyster production, which takes place in subtiadl areas, covered by ice during winter.

Some constraints are common to all countries. First of all good quality water is a continuing requrement as soon as shellfish production begins. Toxic products or pathogenic organismsrequirement as soon as shellfish production begins. value of the molluscs. Antifouling paints containing some TBT (tri butyl tin) have been reported to be responsible for shell abnormalities and spat collection failures on the French coast. In Japan, toxic plankton may produce mass mortalities of various bivalve species. The second point is also related to human health considerations and any problem occuring in a population may lead to consumer resistance and loss of markets, as appears to have happened in Italy.

Most of the countries indicate the existence of some need for technological improvements. This is related to a low level of mechanisation for a labour intensive activity.

Other constraints are related to the volume of the national production. The biggest producers all mentioned the occurence of epizootic diseases and red tides, and overstocking is also a problem encountered in such countries.

Site accessibility and availability seem not to be so clearly linked with the scale of national production, probably because of two different reasons.

National regulations vary greatly and while it is apparently very difficult to obtain a permit for mollusc cultivation in the United States, Japan did not mention any difficulty concerning site accessibility, in spite of a very large mollusc production. In some countries the large number of people involved in mollusc cultivation is reflected by their economic and social strength, so that competition for space or environmental quality may actually assist shellfish culture activities.

Last, but not least, the economic possibilities and restrictions seem to be specific for each country. In the United Kingdom, the market for shellfish products remains limited, and the possibility of product transformation in ready-to-cook meals has been suggested as a mean to promote it. But advertisement campaigns could push the demand beyond the present production possibilities, and increase sea food imports. Another example of marketing problems has been revealed in Italy, where human health was threatened by contaminated mussels. Despite the passage of several years, the consumers' fears are still alive, and the Italian demand remains low, even though sea food comsumption was an old tradition, especially in the southern part of the country.

Biological potential should not be confused with economic possibilities, even for the countries having a large market as long as profitability is the main aim. To maintain and increase the national income from shellfish culture, the efficiency of production management should be improved. Today, the most important point seems to lie with production statistics. First, the capture yield should be separated from the cultivated harvest and reliable statistics should be obtained on actual production. This should concern local production in each area for each species, and take into account the transportation between different areas or countries. Such statistics could allow better management either for the differents areas or for the various products, at a nationwide level. Finally the design and implementation ofa good national data network collection is recommended.

REVUE ECONOMIQUE DE LA CONCHYLICULTURE

J.P. TROADEC *

Objectif. Définir l'importance économique et sociale de la conchyliculture et évaluer son potentiel d'expansion en identifiant et en classant les contraintes majeures et les voies de recherche et de développement succeptibles d'y contribuer.

Les rapports montrent que l'importance économique de la conchyliculture est très variable entre les pays participants. Ces différences sont relatives au volume de production qui varie considérablement d'un pays à l'autre, mais aussi aux méthodes d'évaluation. Ainsi, un point très largement discuté concerne les courbes de production qui incluent souvent, sans distinction, les coquillages de pêche et de culture.

La conchyliculture est fondamentalement un mode d'exploitation extensif, similaire aux élevages terrestres extensifs. Cependant, les degrés d'intervention varient considérablement d'un pays à l'autre pour contrôler et améliorer la production. Le système le plus évolué se trouve au Japon où l'écosystème naturel est modifié non seulement en favorisant l'ensemencement, mais aussi en luttant contre les compétiteurs et les prédateurs et en érigeant des abris. L'exemple typique concerne la coquille St-Jacques dont la production des stocks naturels est passée de 30 000 tonnes à 100 000 tonnes grace à l'intensification des ensemencements en juvéniles et à l'élimination des étoiles de mer.

Données de production

Pour les différents pays, la production culturale est significative pour peu d'espèces de mollusques en regard des apports totaux spécifiques. Les productions nationales des principaux mollusques indiquées dans le tableau I sont exprimées en tonnes (poids total de l'animal).

Les principales productions des pays présents au groupe de travail se rapportent à trois espèces d'huîtres : Crassostrea gigas, C.virginica et Ostrea edulis. Cette dernière, d'une haute valeur commerciale, est sujette, dans certains pays, à des épizooties chroniques.

Les quantités produites par l'élevage fluctuent largement en fonction de la tradition conchylicole de ces pays et de la taille des marchés nationaux. Pour le Canada, la culture d'O.edulis reste à un niveau très bas de production. En France, l'huître du Pacifique représente le principal élevage, les autres espèces (C.angulata et O.edulis) ayant été pratiquement décimées par des maladies. En Allemagne, la culture des huîtres est presque insignifiante et les potentiels sont limités. L'Italie, en absence de marché, expédie sa production vers l'Europe du Nord. Le Japon reste l'un des premiers producteurs d'huîtres avec un tonnage supérieur à 250 000 F. En Angleterre, leur culture dépend des gisements naturels qui servent à approvisionner les parcs. En outre, le marché national d'huîtres vivantes est peu important. Les Etats Unis cultivent uniquement 20 000 T qui représentent un dixième de sa production huîtière.

Les apports d'huîtres cultivées, issues de collecteurs et élevées jusqu'à la mise en marché, sont estimés à 490 000 T pour l'ensemble des pays participants. D'après les données biologiques, la production potentielle serait du même ordre de grandeur que la production actuelle mais elle varierait suivant les pays. Les aspects économiques d'un tel développement seront discutés plus tard.

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* Institut Français de Recherche pour l'Exploitation de la Mer,
Direction des Ressources Vivantes, 66 avenue d'Iéna, 75116 **Paris**, France

La mytiliculture est très souvent au deuxième rang des productions conchylicoles derrière l'ostréiculture. Elle a été développée en Europe, en raison d'un marché plus favorable qu'en Amérique ou au Japon. Une lente extension récente est cependant notée dans ce dernier. La mytiliculture croît actuellement en Italie et en Allemagne ; dans ce dernier pays, la production moyenne de 15 000 T en 1982 a été doublée au cours de 1983. L'Angleterre produit uniquement de la pêche. Au Japon la mytiliculture a été limitée par l'existence d'une toxicité qui a entravé la vente et la consommation. Il est utile de noter que l'Espagne et la Hollande, qui ne sont pas membres du groupe, sont les premiers producteurs de moules du monde.

La pectiniculture est en compétition avec la pêche et dépend du captage naturel. L'exploitation de cette espèce peut être augmentée en favorisant le recrutement. Actuellement, seul le Japon pratique la pectiniculture en utilisant des systèmes d'élevage et des techniques performantes. La production de 1982, évaluée à 77 000 T, révèle son importance. Dans beaucoup d'autres pays, des essais de culture sont en cours, soit à partir d'une production d'écloserie, soit à partir du captage naturel. Le Canada, la France, l'Angleterre et les Etats-Unis ont des programmes de recherche et de développement sur la pectiniculture.

Les autres espèces de mollusques cultivés peuvent être regroupées sous l'appelation de "clams". Deux espèces seulement approchent un niveau de production significatif ; le clam, Mercenaria mercenaria, 6 000 T aux Etats-Unis et la palourde, notamment Ruditapes philipinarum et Venerupis semidecussata. Cette culture est encore à l'échelle pilote, avec des productions de 1 000 T et 300 T obtenues respectivement aux Etats-Unis et en France. Pour l'avenir, la vénériculture devrait connaître un développement important en raison de la haute valeur économique des espèces et de l'opportunité qu'elles constituent pour diversifier la conchyliculture.

Valeur des productions conchylicoles

Pour l'ensemble des pays, la valeur totale des apports de mollusques, exprimée en dollars U.S., est plus élevée pour les espèces pêchées (724 millions de dollars) que pour les espèces cultivées (429 millions de dollars). Ce résultat provient surtout de la forte proportion d'huîtres pêchées aux Etats-Unis et des captures de nombreuses espèces au Japon.

Les valeurs de la production conchylicole des Etats-Unis et de la France sont supérieures à 100 millions de dollars par an, tandis que les revenus des cultures et de la pêche sont beaucoup moins élevés pour le Canada, l'Allemagne, l'Angleterre et, à moindre degré, pour l'Italie.

Il est intéressant de noter que les potentiels biologiques pour la culture des mollusques sont élevés dans quelques pays où le niveau actuel de production est bas, tandis que les autres régions ne sont pas susceptibles d'accroître, de la même manière, leur production nationale. Ainsi de forts potentiels existent pour l'huître au Canada, pour l'huître et le clam en Angleterre et pour la moule en France, en Italie et au Japon.

Situation de l'emploi

La situation de l'emploi en conchyliculture est difficile à cerner en raison d'un manque de statistiques sérieuses et du fait de l'emploi à temps partiel résultant des variations climatiques et du marché. Par exemple, la moitié de la production huîtrière française est vendue durant les deux derniers mois de l'année. En conséquence, dans tous les pays, et pour la majorité des produits, ce travail est considéré pour une certaine proportion à mi-temps. Ainsi, selon les données japonaises, une unité de production peut nécessiter 2.5 personnes. Dans plusieurs pays, la conchyliculture est une activité familiale et le nombre actuel d'employeurs est probablement sous-estimé !

Considérant qu'un travail à temps plein équivaut à deux mi-temps, le total de personnes employées pour la conchyliculture, dans les pays membres, serait approximativement de 200 000. Leur répartition est, cependant, inégale entre les pays pour un même niveau de production. La conchyliculture en France et au Japon utilise un nombre elevé de personnes, tandis qu'aux Etats-Unis quelques conchyliculteurs sont succeptibles d'assurer une importante production. Dans les pays à production faible, en phase de développement, le rapport entre la production et la main d'oeuvre semble être soumis à des effets d'échelle, de par la taille plus faible des unités de production.

Contraintes (Tableau 2)

La conchyliculture est toujours soumise à différentes contraintes qui peuvent être repertoriées comme suit :
- liées à l'environnement
- technologiques
- économiques.

Le climat n'est généralement pas considéré comme un facteur limitant. Toutes les espèces ne peuvent être élevées dans toute zone, de par leurs exigences écologiques pour la croissance et la reproduction, mais la diversité des espèces suffit à garantir qu'au moins une d'entre elles sera adaptée à chaque site. L'ostréiculture canadienne fait exception car elle est pratiquée en zone sous-tidale, recouverte par les glaces en hiver. Quelques contraintes sont communes à tous les pays. La première d'entre elles, concerne la bonne qualité de l'eau indispensable dès le début de l'élevage. Les produits et les organismes pathogènes affectent sévèrement la croissance des animaux et ont des répercussions sur leur valeur marchande. L'étain complexé avec le tri-butyl,contenu dans les peintures anti-salissures a été identifié comme responsable des malformations de la coquille et du manque de captage sur la côte française. Au Japon,les marées rouges provoquent parfois des mortalités massives de diverses espèces de bivalves Les considérants sur la santé humaine, mais aussi les problèmes survenant dans une population, peuvent conduire à un desintéressement des consommateurs et à une perte des marchés,comme cela semble été le cas en Italie.

La plupart des pays indiquent l'existence de besoins en technologie. Ceci est lié au faible niveau de mécanisation d'une activité fortement consommatrice en main-d'oeuvre.

Les autres contraintes sont liées aux quantités produites par pays. Tous les plus grands pays producteurs ont relaté la présence d'épizooties et de marées rouges. La surdensité est également un problème pour quelques pays.

L'accessibilité et la disponibilité des sites ne semblent pas être clairement reliées avec la production nationale : les règlements nationaux sont très divers et, tandis qu'aux Etats-Unis il est parfois difficile d'obtenir une autorisation pour la culture des mollusques, cela ne présente aucune difficulté au Japon malgré une forte production. Dans quelques pays,le nombre de personnes vivant de la conchyliculture leur donne un poids économique et un pouvoir politique suffisants dans l'accès aux sites et le maintien de la qualité de l'environnement. La dernière contrainte, mais non la moindre, concerne les ouvertures et les limitations économiques qui semblent être spécifiques à chaque pays. En Angleterre, le marché des produits conchylicoles reste limité ; la préparation de plats, prêts a être cuisiné, a été suggéré comme moyen de promotion. Mais, la campagne publicitaire peut provoquer une demande plus forte que la production, nécessitant ainsi des importations. Un autre exemple de problème de vente de coquillages a été observé en Italie, où des moules contaminées ont entraîné de graves rèpercussions sur la santé humaine. Bien que plusieurs années se soient écoulées les craintes du consommateur sont toujours fortes et la consommation faible, malgrè la forte consommation

de produits de la mer qui est traditionnelle, particulièrement dans le Sud. Le potentiel biologique ne doit pas être confondu avec le potentiel économique même pour les pays ayant un important marché, aussi longtemps que la rentabilité maximale sera le principal but. Pour maintenir et accroître la part du revenu national provenant de la conchyliculture la productivité des entreprises devrait être augmentée. Aujourd'hui, le point le plus important semble être lié aux statisques. Tout d'abord, les productions résultant de la pêche devraient être distinguées de celles issues des élevages et des statistiques fiables devraient être obtenues sur la production actuelle. Celles-ci devraient se rapporter aux productions par pays, pour chaque région et pour chaque espèce, en tenant compte des transferts entre pays ou régions. De telles statistiques devraient permettre d'améliorer, au niveau national, l'organisation des cultures entre les différentes régions, ou pour les différentes espèces significatives. Enfin, la conception et l'implantation d'un bon système de recueil de données nationales est recommandé.

COUNTRY		CANADA	FRANCE	GERMANY	ITALY	JAPAN	UK	USA	TOTAL
Production (tonnes of live weight)									
oysters	captured	-	-		5 000	-	-	121 600	121 600
	cultured	3 400	110 000	600	400	250 000	600	125 000	490 000
mussels	captured	-	10 000	16 000	-	-	5 200	14 500	45 700
	cultured	900	42 000	16 000	100 000	-	800	1 500	161 200
scallops	captured	-	12 200	-	-	100 000	7 800	185 000	305 000
	cultured	-	spat	-	-	77 000	-	-	77 000
clams	captured	-	-	-	-	238 000	-	66 000	304 000
	cultured	-	300	-	200	300	-	4 300	5 100
Value million US $		2.8	127	2.8	53	632	1	273	1091.6
Employment and	full time	2 300	40 000	600	5 500	167 000	700	4 000	220 100
	part time								
potentiel (estimations)	oysters	175 000	50 000	15 000	30 000	30 000	15 000	-	315 000
	mussels	12 000	100 000	15 000	40 000	30 000	15 000	10 000	222 000

Table I : Assessment of national mollusc shell-fish productions in 1983.

Factors \ Country	CANADA	FRANCE	GERMANY	ITALIE	JAPAN	UK	USA
Climatic limits	++		+		+		
Pollution	+	+	+	++	+		++
Red tides	+	+	+	++	+ (toxic plankton)	+	++
Epizootie diseases		++	+	++	+	++	+
Other mortalities	+	+		+	++		
Technology	++	+	++	+	++		+
Overstocking		+++		+	++	+	+
Competition with other activities	+	+	+	++	+		++
Sites evaluatition and tenure	++	+	++	+++	+	+	+++
Skills	++			+	+		
Marketing	+	+		+++	+	+++	++

Table II : Main constraints encountered in shell-fish culture production and development.

THE CULTURE OF MOLLUSCS IN CANADA - AN OVERVIEW

R.E. LAVOIE *

RESUME

Au Canada, on élève l'huître du Pacifique (Crassostrea gigas) et la moule bleue (Mytilus edulis) sur la côte de l'océan Pacifique; sur la côte atlantique, on cultive l'huître américaine (Crassostrea virginica), la moule bleue (Mytilus edulis), l'huître européenne ((Ostrea edulis), et un peu de pétoncle géant (Placopecten magellanicus). La production d'huîtres du Pacifique s'élève à 2,453 tonnes métriques rapportant $1.2 million E.-U. à quelque 300 aquaculteurs. Sur la côte Atlantique, les cultures de l'huître américaine et de la moule bleue produisent respectivement 915 tonnes métriques ($743,000 E.-U.) et 876 tonnes métriques ($802,000 E.-U.). La production totale annuelle de toutes les espèces s'élève à près de 1,800 tonnes de mollusques, ce qui rapporte $1.6 million E.-U.) à 2,000 travailleurs à temps partiel et à plein temps. On estime le potentiel de production annuelle totale de l'huître et de la moule sur la côte du Pacifique à près de 130,000 tonnes, d'une valeur de ($62 million E.-U.) aux prix courants. Sur la côte atlantique, on estime le potentiel de production annuelle totale d'huîtres américaines et européennes, et de moules à 55,800-59,470 tonnes d'une valeur de ($45-48.5 E.-U.) million.

ABSTRACT

Canadians grow Pacific oysters (Crassostrea gigas) and blue mussels (Mytilus edulis) on the Pacific Coast, and Americans oysters (Crassostrea virginica), blue mussels (Mytilus edulis), European oysters (Ostrea edulis), and some sea scallops (Placopecten magellanicus) on the Atlantic Coast. Pacific oyster production amounts to 2,453 metric tonnes worth $1.2 million U.S. to approximately 300 participants. On the Atlantic Coast, culture of the American oyster and the blue mussel produces 915 metric tonnes ($743,000 U.S.) and 876 metric tonnes ($802,000 U.S.) respectively. Annual total production of all species amounts to nearly 1,800 tons of molluscs worth $1.6 million U.S. and involving 2,000 part-time and full-time workers. Together, oyster and mussel culture on the Pacific Coast have the potential to produce at least 130,000 tonnes worth $62 million U.S. at current prices. On the Atlantic Coast, American and European oysters, and blue mussel culture have a combined production potential of 55,800-59,470 tonnes annually worth $45-48.5 U.S. million.

* Fisheries Research Branch, Department of Fisheries and Oceans, **Halifax**, Nova Scotia, Canada, B3J 2S7

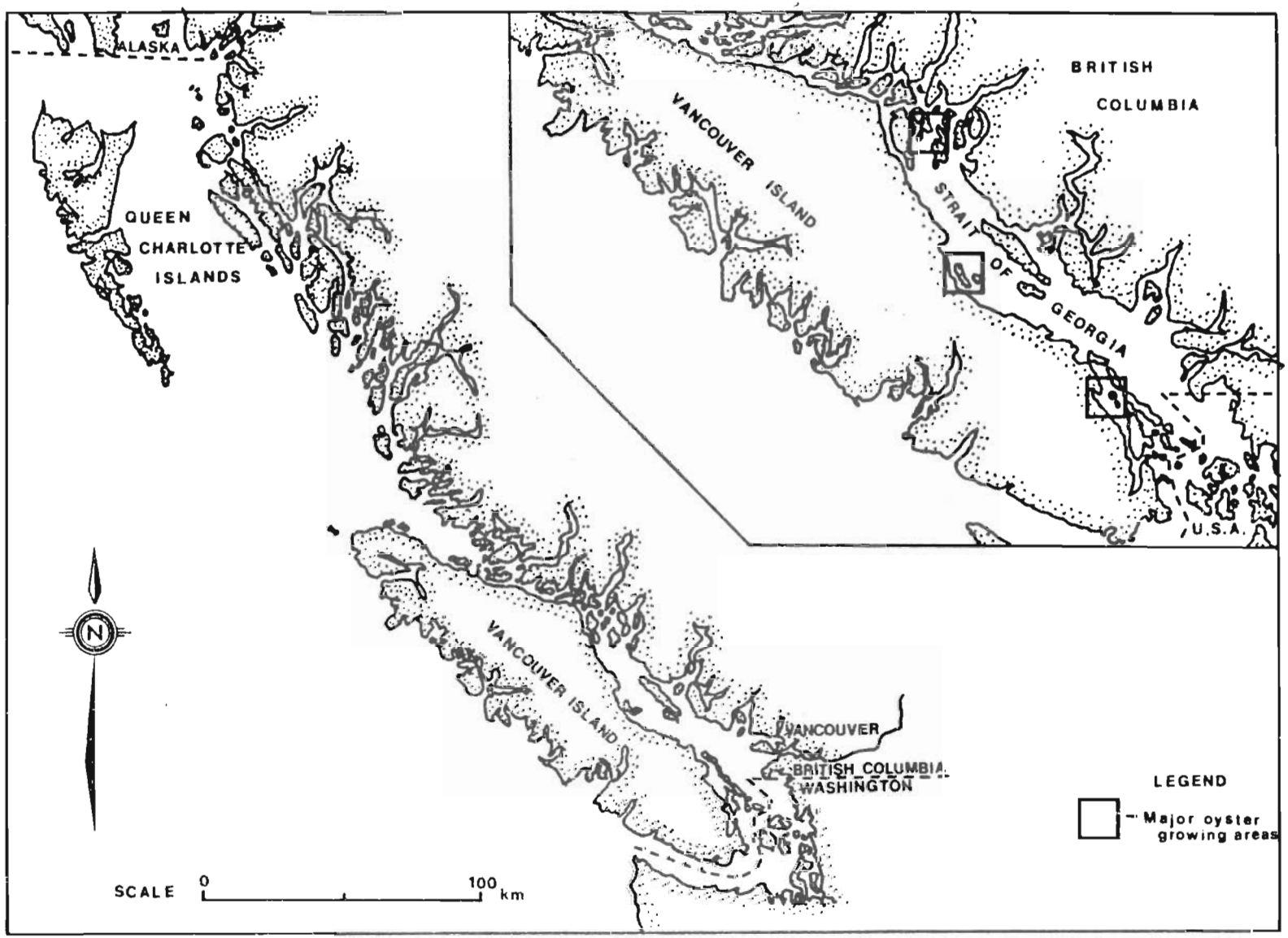

FIGURE 1: Pacific Coast of Canada - Major oyster growing areas (adapted from Bourne and Brett, 1984)

INTRODUCTION

The culture of molluscs in Canada is not very large in terms of people, area involved, landings or value to the Canadian economy. It shows, however, a significant potential for increased production from both the Pacific and Atlantic Coasts.

The first section of this paper applies only to British Columbia. It enumerates which species are currently grown, the location of the important culture centres, production figures or estimates, the landed value, and estimates of the employment generated by the culture activities. Development prospects and constraints are also discussed. Molluscan culture on the Atlantic Coast of Canada is treated similarly in the second section of the paper.

With the exception of the European oyster on the Atlantic Coast, landings of most cultivated species are a mix of cultivated animals and of animals fished from wild populations. To the extent possible, landings from the two sources have been separated and production figures provided are the most recent and accurate estimates of aquaculture production.

1. THE PACIFIC COAST

The invertebrate fauna of the Pacific Coast of Canada is rich and diversified; approximately 800 species of molluscs live along the Coast (Bernard, 1970). However, only eight are harvested commercially. One, the Pacific oyster, has been cultivated for more than 50 years and another, the blue mussel is cultivated on a limited scale and shows good promise.

1.1. The Pacific Oyster

Crassostrea gigas, originally imported from Japan in 1911, is the only species of oyster currently cultivated in British Columbia. The native oyster, Ostrea lurida, and the American oyster, Crassostrea virginica, do not appear to have culture potential on the Pacific Coast.

Pacific oyster culture is practiced in the southern part of the coast, mostly in the Strait of Georgia (Figure 1). Typically, oysters are grown on intertidal bottoms leased from the provincial government. Seed is held for a year on seed ground or planted directly on growing grounds, and take three years or more to reach marketable size. Most of the oysters are shucked and sold fresh. In recent years, other growing techniques have been tried: pin or stake,

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The following abbreviations, units and equivalencies have been used throughout the paper: ha = hectare =2.5 acres; kg = kilogram = 2.2 pounds; mm = millimeter = 0.04 inch; m = meter = 3.3 feet; t, tonne = metric tonne = 2204.6 pounds; U.S. dollar = 1.33 CAN dollar = 9.86 francs = 1980.0 liras = 3.23 marks (W.G.) = 0.90 pound (Br.) = 260 yens.

suspended and tray culture. A half-shell trade developed from tray culture has grown from a production of 104,000 dozens in 1982 to 175,000 dozens in 1984.

The availability of seed is not a problem. Pendrell Sound, located in the northern part of the Strait of Georgia, has the ecological conditions to consistently produce sufficient seed to meet industry needs. Other British Columbia areas with less consistent breeding, and hatcheries capable of supplying either spat or eyed larvae also provide seed. If fully exploited, all seed sources taken together could support a much larger growing industry.

In the past, Pacific oyster production has generally followed years of widely successful natural reproduction. Peak production of 6,195 t took place in 1963. Paradoxically, the very few years of highly successful natural breeding appear to have had a detrimental effect on the culture industry. Lease holders harvested cheaper wild oysters when available and neglected systematic seeding and cultivation of their leases. Once the wild stocks were depleted, they found their understocked leases incapable of sustaining production levels. In 1983, production amounted to 2,453 metric tonnes worth $1.2 million U.S. to approximately 300 participants.

Oyster production could be greatly expanded in British Columbia. In 1983, there were 164 lease holders holding 1,425 ha. In 1981, average production from these leases was less than 1.4 t/ha while Quayle (1969) established that 1 ha of oyster ground could produce 18-28 t annually. In addition, ideal conditions for suspended culture exist throughout the province (Quayle, 1971). It has been estimated (Bourne and Brett, 1984) that 610 ha of suitable area in the Strait of Georgia alone using suspended culture could produce 70,000 to 110,000 tonnes of oysters. Together, more efficient bottom culture and suspended culture could produce 125,000 t of oysters annually, 45 times the 1983 combined total oyster production from wild and cultivated stocks. At 1983 prices, this would be worth approximately $54 million U.S.

What then are the constraints preventing the development of this substantial potential? After all, seed acquisition, biology and cultivation methodology are well known; yet, leases are underutilized and insufficiently seeded, and farming practices are generally poor. Reasons are complex, but the most obvious ones appear to be:

- production units are too small to generate full income;
- lack of confidence in the future of the industry. Growers may hesitate to invest in an industry which does not have the political clout to defend its interest against polluters and other conflicting uses of the growing areas;
- profit margins are too small to permit borrowing of capital.

1.2. Blue Mussels

The blue mussel, Mytilus edulis, lives in all parts of the coast of British Columbia. In recent years, it has been cultivated in the southern part of the province, utilizing an adaptation of the string and socks method (Quayle, 1978; Heritage, 1973). Wild seed suspended from rafts in the spring grows from 10 mm to a commercial size of 50 mm of shell length, giving a production of 17-25 kg/meter of rope in 12-14 months (Bourne and Brett, 1984).

The industry is still very small; four growers with leases totalling 15 hectares produced 1.2 tonne of mussels valued at $1.9 thousand U.S. in 1984. The existing technology, the abundant wild seed supply and the availability of growing sites should allow an annual production of several thousand metric tonnes from the southern part of the province alone (Bourne and Brett, 1984).

There are three major constraints which have so far prevented a large-scale development of commercial mussel culture on the Pacific Coast (Bourne and Brett, 1984). These are:

- fouling organisms on mussel strings, especially barnacles and sea squirts;
- heavy summer mortalities of 35-50 mm mussels;
- heavy winter predation by ducks, especially scoters and goldeneyes.

These problems are being addressed. The summer mortality is now believed to be caused by overcrowding and measures are taken to correct it. Duck predation is countered by providing sacrificial crops, deeper water rearing and protective nets. Also on a positive note, venture capitalists are showing an interest in larger operations.

1.3. Clams

Experimental culture of the Butter clam, Saxidomus giganteus, and the Manila clam, Tapes philippinarum, has been attempted but has not resulted in commercial production to date.

Several problems stand in the way of development of a clam culture industry:

- seed acquisition, and protection after planting;
- slow growth (5 years for Butter and 3 years for Manila clams);
- low prices;
- competition from clams harvested from wild stocks.

Although technologically feasible, clam culture in British Columbia does not appear economically viable at present. Further research is required to reduce costs. One experiment underway involves raising Manila clams and Pacific oysters on the same grounds. Another possibility is the use of nurseries to accelerate growth to market size.

1.4. Scallops

Cultivation of several species of scallops is under consideration in British Columbia. These are: Weathervane scallop (Patinopecten caurinus); Rock (Hinnites giganteus); Pink (Chlamys rubida); Spiny (Chlamys hastata); Sea (Placopecten magellanicus); Japanese (Patinopecten yessoensis). The first four species are native; the latter two are exotic.

The main interest is in the Weathervane and Rock scallops because of their large size. At present, seed supply appears to be the major problem standing in the way of commercial culture. No consistent and abundant natural seed collection area has been identified to-date, and seed will probably have to be hatchery produced.

Culture methods used in Japan could probably be adapted along the entire coast of British Columbia, but economic viability under local conditions still has to be assessed.

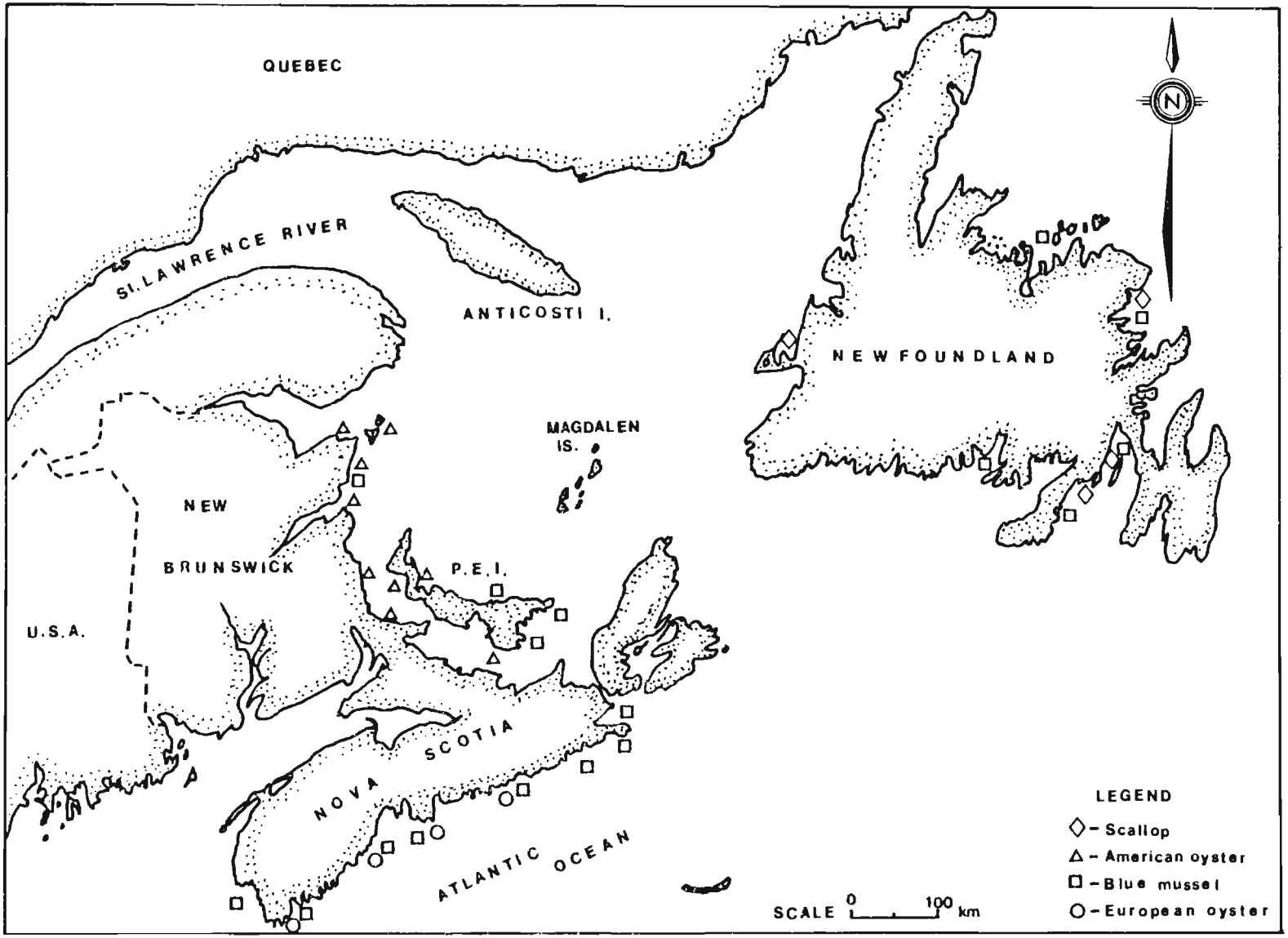

FIGURE 2: Atlantic Coast of Canada - Location of molluscan culture areas

1.5. Abalone

The demand for Northern abalone, Haliotis kamchatkana, fished from natural stocks exceeds supply in British Columbia. The resulting high price ($6.20/kg U.S.) and knowledge of the cultivation success achieved in Japan and California have produced a considerable interest in abalone culture.

So far, a few culture licenses have been granted, a hatchery has been built to provide seed and a pilot plant project has been initiated. First production occurred in 1980. Current production is nil, as the one producer left is suffering from disease problems in his stock.

Abalone could be widely grown on the Canadian West Coast. The main constraints to development appear to be slow growth rate, high natural mortality and the high cost of producing juveniles. The assessment of the feasibility of abalone culture will have to wait until after several more years of trials.

2. THE ATLANTIC COAST

There are five Canadian provinces with coast on the Atlantic Ocean. Aquaculture of molluscs is currently practiced in New Brunswick, Nova Scotia, Prince Edward Island and Newfoundland (Figure 2); Quebec has potential, but no firmly established industry.

Three bivalve species are cultivated. In decreasing order of importance, these are the American oyster (Crassostrea virginica), the blue mussel (Mytilus edulis) and the European oyster (Ostrea edulis).

Although early attempts to introduce the American oyster to the Quebec mainland failed (Corbeil, 1951), more recent work has shown that the province has potential to grow the American oyster (Giguère et Poirier, 1980) and the blue mussel (Giguère et Poirier, 1978) in the Magdalen Islands (located in the middle of the Gulf of St. Lawrence). This potential has not been tested or quantified to-date, and no commercial mollusc farm has been established.

A summary of the area, number of participants, production and value by species and province is presented in Table 1.

2.1. The American Oyster

The American oyster is grown almost exclusively on sub-tidal bottom. Typically, this involves one or several parcels of grounds locally called "leases". This term is used by oyster culturists to designate either the parcel of sea bottom or the official document through which its use is secured.

A lease is a contractual agreement between the Crown and a Canadian individual or corporation, whereby the lessee acquires exclusive rights to grow shellfish on a parcel of sea bottom.

Presently, the initial lease agreement covers a period of 20 years and is renewable. Under the agreement, the lessee has an obligation to mark his leased

area, to pay an annual fee based on area, and to file a mandatory annual report of operations about the work performed on the lease, the amount of seed put on the lease and the amount of shellfish produced from the lease (Anonymous, 1979; Lavoie, 1978). Lease agreements issued prior to 1972 (old policy) carried an annual fee of $2.50 CAN ($1.88 U.S.) per hectare. Post 1972 agreements (new policy) carry an annual fee of $12.50 CAN per hectare ($9.38 U.S.). The fee change was part of a policy revision aimed at encouraging productive lease holders and at accelerating the recycling of grounds held by unproductive and unsuccessful holders. A lessee's rights are transferable through assignments and wills. A lease gives rights to sea bottom only. For suspended culture, a lessee must also obtain an approval or an exemption under the Navigable Waters Protection Act for use of the water column. This, however, does not give the grower any propriatory rights to the water column.

Old policy leases are smaller. Although the old policy covers 73% of the leases, it covers only 54% of the total leased grounds. The new policy encourages the consolidation of small unprofitable leases into larger units. The higher fee under the new policy seems to be having the desired effect by causing a higher turnover of unused bottom, of reducing the overall number of leases and of increasing the average area of leases.

Leases are stocked by relaying natural oysters from mildly contaminated natural beds, picking seed oysters from intertidal or upper sub-tidal natural beds under permit, or using seed from collectors. The first method presently produces the majority of cultivated oysters.

All collector-produced seed comes from natural reproduction. There is no American oyster hatchery in operation at present. In the early part of the 1970's, a systematic five-year program allowed the identification of consistently reliable spat collection sites. Throughout the 1970's, many different types of collectors have been tried: scallop shell strings, shell baskets, plastic discs, various home made wooden collectors and veneer rings coated with cement mixtures, and plastic "Chinese Hats" collectors imported from France. Today, the veneer ring is still used in Prince Edward Island. The Chinese Hat is used in northern New Brunswick, where growers have invented or adapted technology to coat the collectors with cement mixture, hold the spat bearing collectors under the ice during a five-month winter, separate the seed from the collectors and sort it by size, and mechanically seed the grow-out areas.

The potential of the American oyster culture is the best known of the three cultivated species of molluscs. In the Maritime Provinces (New Brunswick, Prince Edward Island and Nova Scotia), there are approximately 6,200 hectares of good oyster ground. Such ground could sustain a production of 22.5 t/ha/year (Medcof, 1961). The public oyster ground occupies 640 hectares, and there are 3,314 hectares presently under lease. If the present leases were fully utilized and all unused good ground brought into production, oyster culture could produce 50,000 t annually, valued at $37.5 million U.S.

The main constraints to development are the climate, a low level of technology and the human element. The cold climate and the long winter result in slow growth and sometimes high winter mortality. Oysters take four to six years to reach market size, resulting in a slow turnover of the invested capital. The high risk and perceived low profitability level have discouraged research and development; technology level is still low. The human element is slow to evolve from harvesting wild oysters to cultivating the sea, although generations of

fishing and low level culture have provided a good knowledge of the ecological factors governing the growing areas. The type of culture, however, lends itself all too well to the social climate of mixed fishery/unemployment insurance which characterizes most of the American oyster distribution range in eastern Canada. Evolution towards high efficiency and yield could be slow.

2.2. Blue Mussels

The blue mussel (Mytilus edulis) is the success story of molluscan culture in Atlantic Canada. Less than 10 years ago, its culture was conducted experimentally by government agencies only. The market was limited and supplied exclusively from natural beds. It is now the favoured species with well established culture operations in Nova Scotia and Prince Edward Island and a promising outlook in New Brunswick and, to a lesser extent in Newfoundland (Figure 2).

Most culture operations use the long line or raft off-bottom culture techniques with rope, plastic collectors and mesh socks. Marketable mussels are produced in 15-24 months. Tenure of growing sites is achieved through shellfish leases similar to those described for the culture of American oysters and approvals or exemption under the Navigable Water Protection Act. In addition to the regular 20-year shellfish lease, potential growers can now obtain conditional two year leases. These conditional leases allow two summers operation to assess the potential of an area as a grow-out site before conducting a professional and often expensive land survey which is necessary to formally describe a parcel of bottom within the formal 20-year contractual lease.

There is a local market in the Maritime provinces, but much of the production is sold in the populated centers of Quebec and Ontario. At present, market expansion is limited by the availability of supply. Current prices are $0.80 - 1.00 U.S. per kilogram.

Constraints to development are the climate, the technology and social factors. Winter ice is a major problem in many areas. It can destroy floatation devices and thus forces growers to lower their suspension devices in the water column to depths which make them immune to drifting ice flows. This raises production costs and makes winter harvesting more difficult and costly. Technologies to address these problems are under investigation. In the meantime, producers have started to coordinate harvesting to minimize the cost of regularly supplying market during the winter.

Technologies are needed for winter harvesting, and/or packing and shipping during warm summer months. Bottom culture and harvesting techniques coupled with predator control methods are needed to allow culture in many shallow water areas, especially in New Brunswick and Prince Edward Island.

Social factors include conflicts between mussel growers and established oyster growers within the same growing areas and conflicts with recreational use of certain growing sites. Oyster growers have objected to the establishment of mussel culture operations for fear that mussel larvae would set on their oysters, literally smothering them. Although this has not been a serious problem to-date, experimental oyster plantings near natural mussel bars in Prince Edward Island have indeed suffered heavily from this factor. Power boat and sail boat users and water-skiers, have objected to the establishment of mussel farms using suspended culture, on the grounds that they create a hazard and restrict their

use of sheltered areas for recreation. Cottage owners have objected to mussel farms for esthetic reasons.

Although still in its infancy, mussel culture in Atlantic Canada shows much promise for the future. The species is widely and well adapted, natural seed is abundant, the growth period to market size is short and the species responds well to cultivation. Markets appear to be expandable, purveyors of venture capital are becoming interested and serious prospective growers are moving in. It appears to be a natural growth area for Nova Scotia which has the least severe ice conditions, and also shows good potential in the other provinces. Annual potential production is estimated at 1,350-2,270 t in Prince Edward Island, 2,250-4,500 t in Nova Scotia, and 1,500-2,000 t in Newfoundland.

2.3. European Oyster

The European oyster (Ostrea edulis) or Belon oyster is the most recent entry for molluscan culture. From a 1969 introduction of Dutch stock via the U.S.A., (Drinnan, 1970), it is now grown at several locations along the Atlantic Coast of Nova Scotia, where water temperature is too low for American oyster culture. The species grows well (3-4 years to marketable size) in off-bottom culture. All seed to-date has been hatchery produced, since there is not wild stock in Maritime waters as yet. The modest 1984 production of 3.3 t (50,000 animals) was of high quality and received a good price in the market place ($0.30 U.S. a piece).

The potential appears to be good. The Nova Scotia coast has many potential grow-out sites, the species has captured the imagination of several researchers working on genetics, nutrition, nursery techniques and husbandry. There seems to be several possible niches for it in the market place: as a luxury product for the half-shell trade in Canada and the USA, and because it is so far free of serious disease or parasites, possibly as under-sized oysters for grow-out in Europe. European gourmets who have sampled the Nova Scotia Belon have generally rated it highly.

In its development plan, the Ostrea Edulis Cooperative Association has set an ambitious annual production target of 700 tonnes by 1991. This would be worth $3 million U.S.

The most immediate constraints to development are seed supply, technical and business know-how, lack of venture capital and possibly some social resistance.

At present, all the seed is produced by two small scale hatcheries. Dalhousie University in Halifax, Nova Scotia, has expanded its experimental hatchery into a seed production operation with government assistance; the other belongs to the Nova Scotia Provincial Government. Together, these two establishments produce approximately 3 million 3-5 mm seed oysters annually, which are sold to growers for $10 US/1000 seed. Although still minuscule by European production standards, this seed should enable a few growers to test several grow-out sites, to improve husbandry techniques, and perhaps reach commercial scale.

All but one of the present growers are part-time operators. For the most part, they came to the business with little knowledge of husbandry techniques and little familiarity with the ecological factors governing their grow-out sites. Through sometimes painful experiences, they have developed a body of useful knowledge which could now become part of an organized training program which should also include small enterprise business skills.

Venture capital is often slow to come to unproven enterprises. Financial assistance for initial capital costs, and the crucial period between start-up and the sale of a first crop may have to be provided by government.

Finally, if European oyster culture develops to a much larger scale, it may have to overcome resistance from commercial fishermen and recreational water users who may resent restrictions to water use made necessary by suspended culture operations.

2.4. Other Species With Potential

Species of molluscs presenting culture potential in Atlantic Canada are the Sea scallop (Placopecten magellanicus), the Bay scallop (Argopecten irradians), and the Bay quahog (Mercenaria mercenaria).

Sea scallop culture has been under consideration in Newfoundland since 1971. Wild spat collected on gill netting or polyethylene film is first held in pearl nets for 6-8 months and then transfered to trays or seeded on the sea-bottom. From 1981, one of two commercial ventures sold 10,000 three-year old scallops and 16,000 seed. Work to-date has demonstrated the biological feasibility of culture. The species occurs naturally in near shore shallow areas where controlled production appears feasible. The high value of scallops will undoubtedly remain an incentive, but the assessment of commercial viability is still several years in the future.

The Bay scallop was first obtained from Milford, Connecticut, in 1977. Under a federal-provincial project, it was quarantined at the Ellerslie Biological Station, Prince Edward Island, through the F5 generation. Limited numbers of hatchery produced seed were introduced to 12 potential grow-out sites in the summer of 1982. Results have ranged from total mortality to 30-50% survival during the winter 1982/83. The 1983/84 winter appears to have killed most of the animals held at grow-out sites. One point is, however, worth noting: animals spawned in the hatchery in the spring actually reached and surpassed the minimum market size of 50 mm of shell height by the end of the growing season in October. This makes the Bay scallop the only molluscan species with a recognized potential to produce a crop within a one-year production cycle on the Atlantic Coast of Canada.

The Bay quahog has been successfully reproduced in a Prince Edward Island Government hatchery and subsequently raised in raceways to a size of 6-7 mm. Experimental introductions in known suitable habitat are being made to test survival and growth, and to assess the feasibility of culture. During the last 2-3 years, approximately 3 million seed quahogs have been introduced on a one hectare plot in the Malpeque/Cascumpeque area of western Prince Edward Island. Observations are continuing. A Nova Scotia Government hatchery produces ½ million seed annually, which is used for experimental work. Seed is planted at a minimum size of 9 mm on small bottom plots to study growth, survival, and site suitability. New Brunswick is conducting a few site assessment studies with seed imported from other areas. Good demand and prices for the species, especially for the Cherry-stone market, should ensure continuing interest in Bay quahog culture, but commercial operations still belong to the future.

3. CONCLUSION

Mollusc culture in Canada still has a long way to go in terms of extensive culture of species already under cultivation, and of achieving the species diversity which would occupy, efficiently, the variety of available habitats.

Currently, Canada grows Pacific oysters and blue mussels on the Pacific Coast, and American Oysters, blue mussels, European oysters and some sea scallops on the Atlantic Coast.

Canadian growers are responsible for nearly 1,800 tonnes of annual production worth $1.6 million U.S. to the Canadian economy, and involving 2,000 part-time and full-time workers. Together, oyster and mussel culture on the Pacific Coast have the potential to produce at least 130,000 tonnes worth $62 million U.S. at current prices. On the Atlantic Coast, American and European oysters, and blue mussel culture have a combined production potential of 55,800-59,470 tonnes annually worth $45-48.5 million U.S.

There are still many areas of potential pitfalls on the road to development (Cook and Drinnan, 1984). Some important ones such as species and site selection, site tenure, water quality, regulations, financing, technology and climate create uncertainties which deter many potential growers. Even their legal rights over their own crop are subject to question for off-bottom culturists (Wildsmith, 1982).

All these potential problems, however, are usually discounted by the aquaculture enthusiasts. For many, it is the attraction of a healthy way of life in daily contact with nature. For others, it is the challenge and spirit of free enterprise. For others still, it is the feeling that the final breakthrough is finally at hand.

Whatever the complex chemistry which will bring success, it will undoubtedly rest heavily on the human element. We now have learned the hard way that aquaculture is not a quick fix for the unemployment problems of unskilled workers. In the Canadian context, the successful aquaculturist needs many skills: a mastery of the biology and ecology of the chosen species, a realistic approach to business and social realities, an ability to deal with governments and a fair bit of staying power.

Positive signs are now starting to appear. Young, well-educated entrepreneurs are appearing on the scene, and they aggressively and systematically overcome the growing pains of their budding enterprises. Some venture capital is moving in. Stories of aquaculture successes in Europe and the Far East are filtering in through the media and specialized publications. The concept of coupling molluscan and non-molluscan aquaculture is being tested. Government agencies at all levels and universities are seeking a new cooperative approach amongst themselves and with the industry, to address the needs in the fields of research, organization, technology development and transfer, training and finances. Mollusc aquaculture appears on the verge of a major development which will bring growth and employment to both the Atlantic and Pacific coasts of Canada.

TABLE 1. Summary of Molluscan Culture on the Atlantic Coast of Canada

Species	Province	Area (ha)	Participants	Production (t)	Value ($000 U.S.)
C. virginica	N.B.	1,060	800	295	246
	N.S.	441	60	150	125
	P.E.I.	1,633	1,000	470	372
	Total	3,134	1,860	915	743
M. edulis	N.B.	204	20	90	82
	N.S.	304	48	450	410
	P.E.I.	700	53	186	175
	Nfld.	?	15	150	135
	Total	1,208	136	876	802
O. edulis	N.S.	?	9	3.3	20
INDUSTRY TOTAL		4,342	2,005	1,794.3	1,565

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MOLLUSCAN SHELLFISH CULTURE IN THE UNITED STATES - A PERSPECTIVE

J.E. HANKS *

RESUME. Même quand les pratiques communes d'aquaculture, tel que le transfert des stocks en régions meilleures pour la croissance, le semis de coquilles à proximité des bancs d'huîtres pour le captage du naissain naturel et l'éradication des prédateurs, sont inclus, l'aquaculture joue un rôle modeste dans la récolte commerciale des mollusques aux Etats-Unis à présent. Les chiffres de production disponibles pour 1983 dénotent les proportions de "capturé" à "cultivé" d'environ 2.5:1 pour les huîtres, 11:1 pour les palourdes dures, 9:1 pour moules, avec zéro de production cultivée pour les pétoncles. Pour évaluer les efforts de culture par rapport aux pêcheries, ce compte rendu discute trois pêcheries de coquillages en exemples : deux (huîtres et palourdes dures) ont beaucoup de production cultivée, et une (palourde surf) n'a pas de production cultivée mais pour celle-ci un système d'aquaculture expérimental est à peu près complet. La recherche en cours pour le développement d'un système d'aquaculture pour les pétoncles baie (Argopecten irradians) est décrite ainsi que le potentiel considérable de production de cette espèce. Les données statistiques sur la production et la valeur de ces mollusques, capturés et cultivés, sont fournies, et par comparaison celles de plusieurs espèces de crustacés et de poissons (marin et eau douce). On présente les recommandations du Conseil National de Recherche, le Comité d'Aquaculture, avec leurs résultats en regard des contraintes et des opportunités pour l'aquaculture. La critique de l'Acte d'Aquaculture de 1980 et du Projet de Développement de l'Aquaculture Nationale est faite pour évaluer la situation de l'aquaculture aux Etats-Unis, et on fait un bref compte rendu du niveau courant d'activité fédérale en aquaculture marine comme base pour le développement futur. Enfin, il y a une liste de références qui fournissent des données plus détaillées sur les pêcheries et l'aquaculture, et d'autres sujets cités dans le rapport.

ABSTRACT. Even when common aquacultural practices, such as relaying of stocks to better growing areas, shelling of grounds for natural spat collection and predator control, are included, aquaculture plays only a modest role in the commercial harvest of mollusks in the United States at the present time. Production figures available for 1983 indicate ratios of captured to cultured of approximately 2.5:1 for oysters, 11:1 for hard clams, 9:1 for mussels, with zero cultured production for scallops. To appreciate culture efforts in relation to the capture fisheries, this report discusses three major shellfisheries as examples: two (oysters and hard clams) which do have considerable cultured production, and one (surf clams) which has no cultured production but for which an experimental aquaculture system is nearly completed. It also indicates the research in progress for development of a bay scallop aquaculture system with the potential to significantly increase production of this species. Statistical data on production and value for these mollusks, captured and cultured, are provided as well as for several species of crustaceans and finfish (marine and freshwater) for comparison. The recommendations of the National Research Council, Committee on Aquaculture, are presented along with their findings concerning the constraints and opportunities for

* National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460, U.S.A.

aquaculture. The Aquaculture Act of 1980 and the National Aquaculture Development Plan are reviewed to indicate the status of aquaculture in the United States, and the present federal level of marine aquaculture activity is outlined as a basis for future development. Finally, there is a list of references that provide information for those interested in more detailed accounts of both the capture fisheries and aquaculture and other material cited in the report.

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mots-clés : huître, C. virginica, C. gigas, palourde dure, M. mercenaria, palourde surf, S. solidissima, pétoncle baie, A. irradians, aquaculture ...

key words : oyster, C. virginica, C. gigas, hard clam, M. mercenaria, surf clam, S. solidissima, bay scallop, A. irradians, aquaculture ...

OYSTERS

Three species of oysters are used commercially in the United States, but only two, the American oyster (Crassostrea virginica) and the Pacific oyster (Crassostrea gigas), actually make up better than 99 percent of the total U.S. production. The other species, the Olympia oyster (Ostrea lurida), has only a minor production, less than 1 percent of the total, but does support a small industry in the Pacific Northwest. A fourth species, the European oyster (Ostrea edulis), which was introduced into the U.S. from Holland during the 1940s, has no significant production at present. It is, however, considered a potential candidate for commercial aquaculture in northern New England and on the Pacific Coast and is under experimental development in both areas.

AMERICAN OYSTER (Crassostrea virginica)

The Fishery

This species occurs along the Atlantic and Gulf coasts of the U.S. and has some production from the Gulf of St. Lawrence (Canada) to Texas and extending into Mexican waters. This oyster was a source of food for American Indians in pre-colonial times and massive shell piles still exist in estuarine areas attesting to the large numbers consumed. Oysters were also an important food for the early colonists since they were abundant and easily collected in the shallow tidal waters of bays and river mouths. The American oyster is one of the most valuable of our commercial mollusks and at the peak of production in the late 1800s just over 1,155,000 metric tons[1] (live weight) were harvested (Engle J.B. 1970). Intensive fishing reduced the natural stocks over the next half a century and by 1968 production had declined to about one-third of this amount. Data for 1983 show a production of just over 300,000 metric tons valued at about $67 million U.S. (Table 1). With this general decline in harvest, demand exceeds supply, keeping prices high. More U.S. plants produce oyster products than any other single fishery product and some 10,000 people are employed in the oyster industry (Sellers M.A. and Stanley J.G. 1984).

In addition to overfishing of oyster stocks, production declines have resulted from such adverse natural factors as droughts and floods which modify the environmental requirements for reproduction and growth causing heavy mortalities of seed and adult oysters. Storms to hurricane strength inflict direct damage to oyster beds through burial of oysters by transported substrates and the abrasive action of disturbed sand and gravel sediments can kill large numbers of recently set oysters. Extensive shoreline development has directly reduced the amount of oyster growing areas available to the industry or altered the seawater quality sufficiently to deter or eliminate successful production. This has been a major factor in many states with losses up to one-third of their coastal wetland areas over the past 20 years to fill and construction projects.

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1 Unless noted otherwise, all production data provided in this report are in metric tons of live weight. However, since U.S. fisheries statistics for mollusks are collected only as edible meat weight in pounds, the metric ton figures are based on conversion from meat weight in pounds to metric tons by an average meat weight to shell weight factor and, therefore, not considered as realistic as the initial data in pounds.

Oysters of all age groups, particularly the smaller sizes, are subject to a variety of predators that take a serious toll. Boring snails, mainly the oyster drill (Urosalpinx cinerea), starfish (Asterias forbesi) and a marine flatworm (Stylochus ellipticus), are the primary enemies but crabs and some bottom fish feed on oysters contributing to the overall predation losses. Other marine organisms, as jellyfish and some pelagic fish, prey on larval oysters during the swimming period and many sessile filter-feeding animals, including other shellfish, ingest larval stages.

Oysters are also susceptible to a variety of diseases and parasites. A fungus (Dermocystidium marinum) is infectious over most of the Middle and South Atlantic growing areas, and into the Gulf of Mexico causing serious losses. A protozoan organism (Minchinia nelsoni) is responsible for the MSX disease which caused extensive oyster mortalities in Delaware Bay in 1957 and in Chesapeake Bay in 1960 (Andrews J.D. 1968) and still poses a problem with recurrent mortalities. Since the larval oyster must have a clean, hard surface for attachment and growth, several marine organisms actually compete for the available setting space, thereby reducing the density of setting and subsequent survival. Major among these are the slipper limpet (Crepidula), jingle shell (Anomia), edible mussel (Mytilus edulis), as well as several species of barnacles.

While there is some oyster production in most states along the Atlantic seaboard, the major fisheries occur in Long Island Sound (Connecticut and New York), Chesapeake Bay (Maryland and Virginia), and the Gulf states (west coast of Florida, Alabama, Mississippi, Louisiana and Texas). Each area differs in growing and harvesting procedures, gear used, and products, and is treated here separately.

Long Island Sound

This industry has traditionally been a private fishery with the bulk of the acreage in use under lease from the states, and oyster companies have considerable capital investment in vessels and dredging equipment. Oyster farming has reached the most advanced level in this area with preparation of grounds and shell plantings to collect set, application of predator control methods, thinning and transplanting of stocks to superior growing areas and, in some cases, the use of shellfish hatcheries to produce seed stocks. Production in Long Island Sound has gone from a high of about 96,000 metric tons in the late 1890s through a steady decline, reaching an average annual production of 5,500 metric tons in 1977 (National Fishery Statistics Program 1984). It has shown some improvement, however, in recent years with a production in 1983 of 6,346 metric tons valued at $4.2 million U.S. (Volk J. CT Div. Aquaculture pers. commun.). Persistent setting failure of seed oysters has been a major reason for this decline with 7-8 years between successful commercial levels of setting and survival not uncommon. There are a few areas of public fisheries, generally under local management, where oysters are fished with tongs, rakes or small dredges, and sold to nearby markets or, more often, collected as seed oysters and sold to the industry for replanting and further growth. The bulk of the harvest is taken by powered vessels using dredges with the catch dumped on deck for sorting to commercial size and select quality. Small oysters and debris, along with sediments collected in the dredge, are shoveled or hosed overboard to the growing beds. Oysters are then transported to shore plants and most are washed, sized and packed for shipment in the shell to markets and restaurants in major cities as Boston, New York, and Philadelphia. Some stocks are shipped to other areas, mainly New Jersey, for shucking and returned to Connecticut and New York for sale as raw meats for use in stews or other cooked products. Competent shuckers in the Long

Island Sound area are very limited in number these days; hence, the use of shucking houses elsewhere to accomplish this task even though it adds a cost to the end product.

Chesapeake Bay

Traditionally, Chesapeake Bay has been the leading producer of oysters in the U.S. In 1966, somewhat more than 134,000 metric tons of oysters were taken from the Maryland and Virginia waters, representing about 40 percent of the total U.S. production. Nevertheless, this is far less than past production in the early 1900s when nearly 513,000 metric tons were harvested (Matthiessen G.C. 1970). Serious mortalities occurred in the 1960s in the lower portion of the Bay, Virginia and Maryland, from the MSX disease, which reduced the harvest and eliminated spawning stocks in areas not generally fished, impeding natural reproduction for reestablishment of commercial stocks. This situation has fluctuated since then with some increases in production, but the recurrence of mortalities is still a limiting factor and the industry has never recovered to pre-mortality production levels. Predation and severe storms cause losses of oysters but are not as damaging to oyster stocks as in other major producing areas. Increased pollution, both domestic and industrial, of the Bay is a major concern to oyster production in recent years accounting for some level of reproduction failure and a direct loss of oyster habitat. The Chesapeake Bay fishery is largely a public industry with only about 10 thousand acres under lease in Maryland compared to almost 350 thousand acres maintained as public grounds. Virginia, with a stronger management attitude, still has only about 40 percent of its nearly 350 thousand acres of oyster grounds under private lease arrangement. Both states subsidize the fishery to some extent in order to maintain its public character with programs for dredging and planting of shell to collect set for rehabilitating the natural beds. The majority of oysters are harvested by tonging but some dredges operate under permit mainly in Virginia and a few in Maryland. In Maryland dredges can be used only when the vessel is under sail, i.e., no engine power is allowed when fishing, certainly more for nostalgic reasons than efficient production but with the purpose of maintaining the industry for the waterman as a public fishery.

In contrast to the Long Island Sound half-shell product, the majority of oysters produced in Chesapeake Bay are shucked and sold as raw meats although some are breaded for frying. In recent years, a fairly large quantity of smaller oysters has been sold to the soup industry. These bring a low price which has assisted in stabilizing the industry at a time when the larger oysters are in short supply due to disease and pollution losses.

The Gulf Coast

In comparison with the declines indicated for Long Island Sound and Chesapeake Bay, the oyster industry along the Gulf Coast is unusual in that production has been relatively stable over the past 30 years. Production is on the order of 126,000 metric tons annually valued at $19 million U.S., so that nearly half of the total U.S. production comes from this area (National Fishery Statistics Program 1984). It is estimated that this is only a fraction of the potential since the industry is not well-organized, with little emphasis on marketing techniques or quality control. The fishery, except for Louisiana, is largely a public operation which does not encourage capital improvement or the use of modern farming methods to any degree. Louisiana does have private leasing of oyster grounds, ranging from 100 to 1000 acres, with over 130,000 acres under lease and additional underwater land in the process of survey for leasing; most oystermen operate their own private beds.

Oysters produced along the Gulf Coast are sold as raw shucked, steamed and canned or marketed in the shell to oyster bars for the half-shell trade. The latter are selected for superior quality and receive the highest price but make up only a minor portion of the final product. Most oysters are harvested from public reefs by tonging; dredges are used on leased areas in some states. Pollution from domestic sewage and oil spills has endangered or eliminated once productive beds and periodic hurricanes cause heavy damage. The most serious oyster predator in the Gulf is the drill (Thais haemostoma) but fungus diseases, as Dermocystidium, also take a heavy toll, particularly in the summer months. On the other hand, fast growth, attributed to generally warm water temperatures year-round, and high levels of phytoplankton in the water lead to a commercial size in 12 to 16 months allowing a crop at least by 2 years of age as compared to 3-4 years in northern waters. Fast growth, however, does account for a poorer shaped oyster and is the reason more of the production is handled in the lower priced shucked form rather than as half-shell stock.

PACIFIC OYSTER (Crassostrea gigas)

The Fishery

Initially, the Pacific Coast oyster industry was based on the native Olympia oyster (O. lurida), and the American oyster (C. virginica), which was shipped from the Atlantic Coast, planted out for a period of time and then harvested. California was the center of the fishery for the latter species with production in the late 1800s on the order of 16,045 metric tons (Matthiessen G.C. 1970). The transplant procedure was necessary since this oyster did not reproduce in Pacific Coast waters due to comparatively low water temperatures. Ecological changes resulting from dredge and fill operations in coastal areas and increased pollution decreased successful growth and survival of the transplanted stocks to the extent that this fishery was virtually eliminated by 1930 although a limited amount is still handled in this manner due to the market demand for quality half-shell oysters.

While the Olympia oyster has a ready market, natural populations once abundant in the coastal waters of the Pacific Northwest also declined for similar reasons, and it supports only a limited fishery with production of less than 1.0 percent of the total U.S. oyster harvest. It is a slow growing species, sensitive to excessive heat or cold necessitating its being grown in diked areas rather than cultured intertidally. Although it brings a price of $60.00 or better for a gallon of shucked oyster meats, 1200 to 1500 oysters are required to obtain a gallon of meats, making labor costs high for processing.

With a steady demand for oysters on the Pacific Coast, the industry looked elsewhere for its oyster stocks, leading to a successful introduction of C. gigas from Japan in 1919 and commercial production starting in the 1920s. As a hardy and rapid growing species, reaching a length of six inches or better in 2-3 years, it took well to intertidal culture practices and soon formed the basis of the oyster industry on the Pacific Coast. Seed was imported annually from Japan in cases holding 15 to 30 thousand oysters as low water temperatures inhibited natural reproduction in most areas. However, some areas proved suitable for spawning and natural populations became established from which seed stock could be obtained. Economic changes, combined with an expanding international market for seed, have increased the cost of seed produced in Japan limiting this practice and making U.S. produced seed competitive in price. Even so, successful natural sets are irregular and hatchery operations now supply the bulk of the seed stock to the Pacific Coast industry (Chew K.K. and Donaldson J.D. 1985).

This fishery is essentially private with grounds leased from the states - Washington, Oregon and California - and, as a result, is progressive in its operations with both bottom and rack and raft suspension culture in use although bottom culture is still the predominant method. Harvesting is done by hand or fork at low tide or by dredge from a vessel at high tide. Predator problems exist and losses of oysters occur from the oyster drill (Ocinebra japonica), now endemic but originally introduced by accident from Japan with imported oyster seed, as well as crabs and fish.

Aquaculture

Of the marine mollusks, the American oyster, C. virginica, is the primary species that has been studied for purposes of artificial cultivation. Commercially-oriented efforts initiated in the U.S. in the 1920s (Wells W.F. 1926) with the recognition that successful recruitment of an annual set was perhaps the oyster industry's greatest problem, led to successful rearing of fertilized eggs, stripped from ripe female oysters, through larval development to metamorphosis and setting. This experimental work was supported by the oyster industry and conducted under early hatchery conditions. Wells' method for rearing larvae depended upon the natural phytoplankton supply in the seawater as a food source. Following similar efforts by others, an intensive study, aimed at developing a standard methodology, was undertaken by Loosanoff V.L. and his associates starting in the mid-1940s at the Milford Laboratory, U.S. Bureau of Commercial Fisheries (now National Marine Fisheries Service), Milford, Connecticut. This group established routine and dependable procedures for conditioning oysters to ripeness, inducing spawning and fertilization, rearing larvae to setting and growth of newly-set spat. Their methods differed mainly in that live algal food, cultured in the laboratory, was provided for larval nutrition. This, plus temperature control of the laboratory seawater, made it possible to conduct hatchery operations on an annual basis and opened a potential for the reliable commercial production of oyster seed. Details of the development of these techniques, as well as the contributions of earlier and contemporary workers, are provided in an extensive review (Loosanoff V.L. 1971). Davis H.C. (1971) presented a similar review of equipment and facility requirements, as developed at Milford Laboratory, for environmental control of the oyster culture system.

The mass culture of algal species for use as larval and juvenile food is an essential phase, whether used as the sole source or supplemental to natural phytoplankton levels,and considerable research has gone into this aspect of successful molluscan aquaculture. Ukeles R. provided detailed reviews on this from a larval nutrition viewpoint (1971 and 1976a) and for algal culture methodology (1976b and 1980).

Commercial and experimental hatcheries now exist, mainly on the Atlantic and Pacific coasts, applying those methods to produce several species of oysters and clams. Some companies use this production for planting on their own grow-out areas and market the adult product. Others produce and sell seed to the industry on a per order basis for commercial grow-out. Examples of advertised prices for oyster and clam seed supplied by hatcheries are given in Table 4.

A recent development is the sale of oysters at the eyed-larvae stage to be shipped elsewhere for setting under controlled conditions and for transplant to grow-out areas at some point after setting. This procedure allows a large number of larvae to be shipped in plastic bags of seawater and reduces time, care and cost at the producing hatchery; but it does place any risks for successful setting conditions in the hands of the purchaser who must have adequate facilities for handling the larvae.

Hatcheries are expensive, both in capital investment and operating costs, and while there appears to be general industry interest in buying seed for grow-out, dependency on others for seed poses problems similar to that of dependency on natural seed production. If the hatchery source fails or the cost of seed becomes prohibitive, the grow-out side is out of business at least for a period of time. The most practical approach to a dependable aquaculture system still appears to require a hatchery to insure the availability of seed for one's own operation.

HARD CLAM (Mercenaria mercenaria)

The Fishery

The hard clam or quahog fishery dates to the depression years of the 1930s when considerable amounts were harvested, although they had been used as a food source since colonial times and earlier by American Indians as evidenced by their presence in old shell piles. This species ranges from the Gulf of St. Lawrence (Canada), along the Atlantic Coast and into the Gulf of Mexico. Hard clams occur intertidally throughout in bays and estuaries and subtidally to depths of about 15 meters on portions of the Atlantic continental shelf. However, the commercial fishery is centered in southern New England and the Middle Atlantic states, with the highest commercial production levels in Massachusetts, Rhode Island, New York, New Jersey, and Virginia and with lesser amounts in Maine, Connecticut, Delaware, Maryland, North Carolina, South Carolina and Florida. It is the largest clam fishery in the United States providing employment to 17,000 fishermen, many on a part-time basis, and uses 13,000 vessels (Ritchie T.P. 1977), mostly small boats. Data for 1983 indicate a harvest of slightly over 48,000 metric tons valued at better than $42 million U.S. (Table 1). Hard clams are sold in three sizes: large or chowder (97 mm average length) and the lowest priced are used in clam chowders or cut up as a base for other seafood products; medium or cherrystone (75 mm average length), and small or littlenecks (55 mm average length). The latter two sizes are used as raw half-shell or as steamed clams and command the highest prices. Hard clams are harvested with rakes, hoes or tongs in a hand operation, and a large portion of the production is obtained in this manner by individual fishermen. Subtidal populations are also fished using heavy hydraulic dredges with seawater jetted ahead of the dredge blades to loosen the bottom and allow easier collection of clams in attached metal-ring bags or metal cages. In recent years this type of dredge has been combined with an escalator-conveyor system which brings the clams from the dredge to the boat deck where they are culled to standard sizes with any undersized clams dropped overboard for further growth. This gear is very efficient in waters of 2-5 meters deep, but is not in universal use due to varying state and local regulations that in many cases limit harvesting methods to hand labor excluding any use of mechanical gear.

Most hard clams are sold in the shell in the cherrystone and littleneck sizes. Large clams are processed at shore-based plants using hand shucking or heat treatment to open. The meats are then washed and diced, minced or ground for use in various products.

Predators (as crabs, snails, fish and waterbirds) and pollution, both domestic and industrial, are the major problems affecting the resource. Many areas with abundant populations of hard clams are closed to fishing by health authorities because of high pollution levels.

Some states have employed extensive relaying programs to dredge and move clams from polluted to unpolluted waters where they can cleanse themselves naturally over a period of time and then be harvested for human consumption. Depuration procedures are also in use in some states to cleanse clams taken from moderately polluted waters by chlorination and/or ultraviolet light treatment of seawater in which the clams are immersed for fixed periods. Both procedures allow the use of clam resources from polluted areas and provide for an increase in safe, marketable production.

Management of the fishery is largely at the state and local level and differs considerably between states as to minimum sizes and gear that can be used for fishing.

Aquaculture

An aquaculture system for the hatchery production of hard clams has been available for some time. It is based on methods similar to those used in the culture of oysters but modified relative to differences in biology, mainly that clams do not attach to a substrate as do oysters but rather dig into the bottom and grow to adults. The procedure is to induce spawning, rear fertilized eggs under controlled conditions in a hatchery to setting and then raise them in trays or tanks to small seed clams on the order of 15-20 mm. At that size they are transplanted to growing areas in the field under private ownership or leased to the industry by the states. Such plantings are used to supplement natural reproduction and enhance the resource base or to attempt restocking of grounds depleted by heavy fishing effort or natural mortalities. Since these hatchery produced clams cannot be identified from those naturally produced, evidence is circumstantial that they contribute significantly to actual production. However, they do increase the stock base and, when environmental factors are favorable, should add some amount to the harvest. The industry seems satisfied that the practice does account for increased production.

Fully controlled culture, i.e., fertilized egg to harvest, of the hard clam has been achieved and demonstrated biologically, but has not been shown to be commercially feasible in the various systems attempted for large-scale production. Predators are a serious problem in the field grow-out areas as they consume large numbers of seed clams before they can grow to a size that offers some natural protection. Most efforts at this time are aimed at affording a period of protection for seed clams through the use of surface mats or gravel layers that allow the clams access to the water column for feeding purposes but prevent predators from reaching the clams. Antifouling requirements are also critical since a heavy attachment of plant and animal life to the protective material prevents the clams from being able to feed and grow. Any real breakthrough that results in an economical and practical grow-out procedure would tend to rapidly expand hard clam aquaculture. Large areas, both intertidal and slightly subtidal, are suitable for this type of culture and the market demand for the small-sized clams is nowhere near met by the existing fishery. Data for 1983 show culture production at 4,300 metric tons which is inclusive of production from aquacultural practices, such as relaying of clams from polluted to non-polluted areas prior to harvest, redistributing small clams from densely populated areas to other areas for further growth, etc., at a value of $9.5 million U.S. (Table 3). Only a very small amount is actually produced under fully controlled conditions from hatchery to harvest. Clam hatcheries operating in Massachusetts, New York, New Jersey, Maryland and Florida produce seed clams for sale, as well as for their own use for planting stock for grow-out. Production data and value from these operations are not available.

A manual for growing the hard clam - covering hatchery techniques to field planting and care of the stocks - has been published (Castagna M. and Kraeuter J.N. 1981) and is particularly useful to anyone wishing to start out in such a venture or needing to know details of current techniques and methods to update efforts already underway.

SURF CLAM (Spisula solidissima)

The Fishery

Surf clams are fished commercially on the continental shelf of the Atlantic Coast primarily off the Middle Atlantic states of New York, New Jersey, Delaware, Maryland and Virginia, although the species range is from the Gulf of St. Lawrence (Canada) to Cape Hatteras, North Carolina. The fishery started pre-1940 on a small scale as a source of bait for the hand-line cod fishery. With a change in use to food products for human consumption in the 1940s and 1950s, as clam chowder and fried clams, the fishing effort increased significantly during the 1960s and 1970s aided by surveys of the resource conducted under federal sponsorship and improvements in fishing gear developed by the industry. It currently contributes better than 70 percent of all clam meats used in the United States with a production level in 1983 of nearly 140,000 metric tons valued at about $25 million U.S. (Table 1). Surf clams were initially fished with rakes and tongs, but today they are harvested primarily by vessels of 25 meters or larger using hydraulic dredges. Seawater is pumped through a jetting system ahead of knifelike dredge teeth that dig into the ocean bottom and the clams are collected in metal-ring bags or cages. Although surf clams occur from the coastal beach area to depths of 65 meters, the fishery is concentrated from nearshore to a depth of about 35 meters in bottoms consisting of sand, mixed silty-sand and gravel (Ropes J.W. 1980). While a maximum size of 8.9 inches (226 mm) has been reported, the commercial catch ranges in size from 90 to 135 mm for the nearshore grounds and 135 to 195 mm for the offshore grounds (Ropes J.W. 1982). Processing of surf clams is done at shore-based plants using a heat treatment to separate the meats from the shell and automated equipment to eviscerate and to cut or grind the meats. The meats are washed to remove sand and shell particles and then canned, packed and frozen or packed fresh, depending upon the desired product and use. The fishery is currently under a federal management plan (FMP) that, as necessary to maintain the resource, can close the fishery seasonally, control areas to be fished or limit the catch. It is also under state regulation regarding minimum size to be fished but this is not uniform within the states involved. Overfishing, predators and natural mortalities all contribute to fluctuations in fishery landings, and product demand is generally greater than the fishery can supply. Whether management strategies will overcome these problems to maintain a sustainable-yield fishery is not yet known since the FMP has been in effect only a few years and is modified as stock assessment information improves.

Aquaculture

At present there is no commercial aquacultural production of the surf clam. It is also unlikely that efforts will be directed to that purpose in terms of any fully-controlled production even though the fishery fluctuates and demand is in excess of supply on a regular basis. However, consideration has been given to the use of hatchery produced seed to restock grounds, either depleted from overfishing or which have suffered severe natural mortalities. Such an undertaking would probably have to be funded by a state or federal program as an enhancement strategy since it would involve considerable cost in hatchery facilities and operations with

the seed going into an open, but regulated fishery not suited to interest investment capital. There is also doubt that such an effort would be realistic in biological terms. Given favorable ecological conditions, natural reproduction should restock an area faster than planting seed ever could and with no cost involved; given unfavorable ecological conditions with consequent low-to-zero survival, seeding to restock would appear to be a futile effort and wasteful of funds expended.

Independent of fishery enhancement, there is interest in the potential of an aquacultural system for the surf clam to produce a marketable small-size clam in one year or less. This approach is based on the general short supply of small-size clams, mainly hard clams (Mercenaria mercenaria) and soft clams (Mya arenaria), for the raw (half-shell) and cooked (steamer) trade. Based on the fast growth of young surf clams, it appears feasible to culture this species, using controlled methods throughout, for a totally different product and market than that of the natural fishery. Research and development of such a culture system have been underway for several years at the Milford (Connecticut) Laboratory of the Northeast Fisheries Center, National Marine Fisheries Service, NOAA. Goldberg R. (1980) discusses the experimental studies for ripening and induced spawning, larval culture, and grow-out techniques for post-larvae to a usable size of 50-60 mm in 10-12 months. This system makes use of tray culture of post-set clams at controlled seawater temperatures with supplemental algal food until the clams reach a size of 18 mm. They are then transferred to large fiberglass tanks and grown to a 55 mm size using ambient seawater temperatures and only naturally occurring phytoplankton algae as the food source. Experiments for a final grow-out in protective cages attached to the bottom in open estuarine water have also been conducted and show some promise as an alternative method. While no commercial efforts have been attempted that would provide an economic evaluation, the system seems to have good biological potential. Also, the major experimental operating expenses - electricity and labor - do not seem prohibitive for commercial scale-up.

Complementary technological studies on the utilization of a small-size surf clam were undertaken cooperatively at the Gloucester (Massachusetts) Laboratory of the Northeast Fisheries Center, National Marine Fisheries Service, NOAA. Krzynowek J. et al. (1980) report taste panel results as very good to excellent for all products tested (steamed, breaded and fried, and raw on the half-shell) and fully competitive with equivalent products using commercially fished hard clams (Mercenaria mercenaria) and soft clams (Mya arenaria). Frozen storage of surf clams in the shell and as shucked meats showed no significant taste deterioration on monthly sampling over one year. Chemical analysis during that period indicated that small surf clams provide an excellent source of low fat, high protein seafood.

Certainly, extensive market testing and economic studies will be necessary to determine the commercial feasibility of surf clam utilization but the preliminary indication is good for successful product development.

BAY SCALLOP (Argopecten irradians)

Aquaculture

Although there are significant fisheries for scallops along the Atlantic Coast from Maine to Florida with a 1983 production of about 185,000 metric tons valued at approximately $136 million U.S. (Table 1), the catch is made up of several species: the sea scallop, Placopecten magellanicus, the calico scallop, Argopecten gibbus, and the bay scallop, Argopecten irradians. At the present time, only the bay scallop appears suitable for aquaculture and will be considered in this report without a discussion of the natural fishery.

Factors that make the bay scallop a prime candidate for aquaculture include the high market price compared with a generally low supply, irregularity of natural recruitment, and rapid growth allowing harvest at 10-17 months from the southern to the northern portion of its range. Thus, the bay scallop is unpredictable in terms of the stability of fishable populations, while high price and strong market demand suggest that a reliable, consistent source of supply through aquaculture would find a ready, profitable market.

Hatchery culture methods similar to those for oysters have been available for some time so that conditioning, spawning, larval rearing and setting can be easily accomplished (Loosanoff V.L. and Davis H.C. 1963; Castagna M. and Duggan W. 1971; Castagna M. 1975). The problem with various systems tested has been the grow-out stage. While most bivalve mollusks, as juveniles, are either attached to some surface or dig into the bottom and remain sessile, the bay scallop rests on the bottom and can swim for moderate distances by rapidly opening and closing its shells. This means they must be retained in some manner during the period of growth to harvest. Floats, pens, fences, cages, and raceways have all been used with some degree of success, but each presents practical and/or economic difficulties that have deterred commercial development.

Studies over the past several years at the Milford Laboratory, National Marine Fisheries Service, have concentrated on this grow-out phase, both in raceways and lantern nets, in an effort to determine optimum densities for maximum growth at natural levels of algal food to produce an economic product (Rhodes E. and Widman J.C. 1980; Rhodes E. et al. 1982). For raceway grow-out, a balance of water flow and stocking density is obtainable that allows scallops to reach a market size of 50 mm or greater in less than a single growing season, i.e., on the order of 7-8 months. However, the cost for pumping water makes grow-out to harvest under raceway conditions economically impractical. Their use for lesser growth requirements, as to 10-20 mm for replanting in other systems, is feasible and raceways have advantages for small scallops in that predator presence or fouling is easily observed and can be corrected promptly. Also, as they are land-based, they require only a source of good quality seawater which gives flexibility for site location.

Corresponding studies using lantern nets were then conducted. Initial experiments with free plantings of scallop seed resulted in mortality levels, mainly from crab predation, as high as 90 percent in 14 days or less. Studies were then shifted to using commercially available lantern nets, patterned after a Japanese design used for scallop culture. These are anchored to the bottom and buoyed with styrofoam floats in about 8 meters of water, well below the surface so as not to interfere with boating activities. The nets are stocked with 20 mm scallops and produce 50 mm scallops - the minimum market size - in a single season (approximately 5 months) of grow-out. This combined hatchery-raceway-lantern net system appears biologically and economically feasible and field-scale studies are now in progress to determine density strategies, etc., to attain maximum production levels.

AQUACULTURE IN THE U.S. - CONSTRAINTS AND OPPORTUNITIES

A study conducted in the mid-1970s under the sponsorship of the National Research Council, Committee on Aquaculture, resulted in the publication (National Academy of Sciences 1978) of an extensive review of the current status of aquaculture in this country outlining existing constraints and opportunities. These findings point out that aquaculture has developed more slowly than other food sources in the United

States and is less advanced here than in other technologically advanced nations. Some species are being profitably cultured, while efforts are continuing to expand the number of cultured species. The report notes that current constraints on aquaculture tend to discourage new initiatives and, unless some of these constraints are overcome, real progress will be further delayed.

Analysis of production systems, science and technology, economics, business, law and public administration indicates that aquaculture will have only a minor near-term impact on food production in the U.S. in comparison with other systems. For the future, however, aquaculture will be a means of increasing protein supplies and has the potential to contribute to increased food production. To test this potential, expenditures for research and development will need to be increased significantly.

Constraints on the development of aquaculture tend to be more political and economic than scientific and technological. Advances are needed in all areas but, for overall progress, the essential requirements are policy decisions and administrative actions.

The most serious economic constraints are: low prices or limited markets for products; high prices or limited availability of purchased inputs, such as sites, capital, unskilled labor, and trained managers, and of operating inputs, especially feed, water, seed, energy and chemicals; and the great quantity of purchased inputs necessary to produce output.

The report also stresses that economic analysis of legal and institutional effects on aquaculture development is critical for guidance to the development of public policy. Research should be focused on species that have the greatest potential for acceptance in U.S. or other markets. Because establishment of new ventures in aquaculture will require significant market development beyond the ability of individual firms, federal support is necessary for public and private research on marketing aquacultural products. Prices and availability of sites, labor, feed, seed, and drugs have changed drastically in the past and will surely change more in the future. To allow for adaptation of technology over time, research is necessary on the relationship between potential aquacultural products and the land, labor, capital and operating inputs required to produce the species.

Aquaculture should be eligible for assistance from programs of the Small Business Administration and the Department of Agriculture. In particular, federal flood and disaster insurance, crop insurance, and low cost financial programs should be made available. Government programs generally available to support agricultural activities should also be available to aquaculture enterprises.

There are three primary constraints on the development of successful production systems that affect all types of commercial aquaculture. Two of these relate to gaps in the technology base; the other concerns getting appropriate available technology into use in the industry. It is recommended that priority be given to improved technology for rearing cultured species during the early stages of their life cycle, and for formulating, processing, and delivering food for cultured species, and the construction of demonstration facilities.

Knowledge pertaining to the biology of certain species, to culture technology, and to appropriate site selection is sufficient to permit some enterprises to be profitable. Little information is available, however, on the specific nutritional

requirements of most culturable species at various stages in their life cycle although many cultured species are critically dependent upon the food provided to them. Appropriate diets can help to improve survival rates, growth rates, conversion efficiency and disease resistance. Continued research is necessary to determine the nutritional requirements of culturable species throughout their life cycle.

Populations of aquatic organisms must be cultured in high density to be economically useful. Mass culturing frequently fails, however, because of insufficient knowledge concerning environmental conditions, behavior, and reproduction. Further research is required to improve understanding of mass culture in order to increase control over behavior and reproductive processes so that the necessary stocks of seed or juvenile organisms can be developed.

The great potential of improved breeding programs has yet to be realized for most culturable species of commercial importance. Genetic research in the U.S. has been primarily directed at the salmonids. Mollusks and crustaceans are certainly amenable to the use of genetic techniques. Application of such techniques would improve product quality and the efficiency of the culture process. Expanded research is required on the genetic characteristics of culturable species to develop strains possessing desired characteristics and to preserve natural and domesticated brood stocks.

Effective health management of cultured stock is essential for successful culture. Control of disease in culture systems by means of appropriate prophylaxis and treatment is not yet adequately understood or applied. Known pathogens can cause catastrophic losses, and further culture experience will reveal additional threats from many kinds of organisms. Increased research is needed to improve knowledge of disease organisms and to develop appropriate disease control techniques.

The introduction of exotic stocks and species and the frequent local transfer of stocks create a potential for the introduction of diseases, parasites, competitors and injurious genetic strains. If a safe procedure for such transplants can be developed, improvements in cultured products will result. Procedures must be established for registration of all exotic transfers and for quarantine to prevent introduction of diseases.

Priority areas of research requirements are in nutrition, feed technology, genetics, reproduction, health management, and various aspects of aquaculture systems. Because problems in these areas that relate to aquaculture require extensive research, federal activities should focus on the long-term research and development requirements of aquaculture, rather than on short-term problem-solving.

NATIONAL AQUACULTURE ACT OF 1980

With the enactment of the National Aquaculture Act of 1980, the federal government indicated its support to the development of aquaculture in the United States. The Act assigned to the Departments of Agriculture, Commerce and Interior responsibility for planning, policy, direction and implementation of aquaculture activities and support of private enterprise efforts in this field. Several million dollars (U.S.) were authorized to carry out such programs but no funding has ever been actually appropriated due, in part, to political aspects but primarily to recent budgetary policies adverse to any funding for new projects. All of the ongoing aquaculture research and development and support activities since 1980 have been a

continuation of previously initiated programs at either level or declining annual funding. The Act was of three years' duration but has been extended for two additional years, through September, 1985. It is anticipated that it will either be extended again for another period of time in its original version or, more probably, replaced by a new and revised Act modified to meet economic, political and administrative changes occurring over the past five years.

The Act directed the preparation of a National Aquaculture Development Plan which was prepared by the Joint Subcommittee on Aquaculture (JSA) and published in two volumes in September, 1983. Volume I describes technologies, problems, and opportunities in aquaculture; recommends actions for their solution and analyzes the socio-economic and environmental impacts of growth in aquaculture. Volume II discusses potential and constraints for a number of selected organisms in the format of species plans and also contains an extensive bibliography and list of contributors.

The Plan indicates that private aquaculture development in the United States, except for a limited number of marine and freshwater species, has not occurred at a rapid pace. Although scientific and technological problems still exist, the primary constraints to the expansion of aquaculture are political and economic. Constraints include competition for land and water areas and markets, regulations on federal, state, and local levels, inadequate transfer of information and technical assistance, and uncertainty about profitability. Coordinated and successful action to overcome these barriers has been lacking. Nonetheless, private aquaculture accounts for a significant portion of the supply of some species in the U.S. (Tables 2 and 3). Thus, aquaculture produces over 40 percent of our oysters, most of our catfish and crawfish, nearly all of our rainbow trout, and small quantities of several other species. Total harvest of edible fish and shellfish in 1982 was 1,500,000 metric tons, of which about 179,500 metric tons or about 11 percent of the total, was produced by aquaculture.

Emphasis in the U.S. private aquaculture sector has been on the culture of high-value species, with little commercial activity on the culture of such low-cost fishes as carp or mullet. Profit, rather than an effort to increase the national food supply, has been the prime motivating force.

FEDERAL AQUACULTURE ACTIVITIES

Aquaculture research and development activities with marine organisms have been supported by the Department of Commerce (DOC) through the Economic Development Administration (EDA) and the National Oceanic and Atmospheric Administration (NOAA). EDA has provided funds for aquaculture, primarily as a means toward job creation and to generate or preserve income. These programs have provided various native American groups with approximately $8.0 million for aquaculture development during the past 15 years.

NOAA conducts aquaculture research and development through the National Marine Fisheries Service (NMFS) and the Office of Sea Grant (OSG). Research supported by NMFS is conducted primarily by utilizing in-house scientific expertise at NMFS centers, laboratories, and field stations. OSG supports research through grants to universities and other entities. The technology gained from this research is utilized by private industry for commercial purposes and by public agencies for augmenting natural stocks through enhancement programs.

NMFS conducts research programs at six laboratories and field stations. These programs involve extensive research on salmon nutrition, diseases and improved husbandry techniques; maturation and spawning of marine shrimp indigenous to the Gulf of Mexico and enhancement techniques for marine turtles (Galveston, Texas); diagnosis of diseases of shellfish (Oxford, Maryland); and a variety of molluscan studies on natural diets, genetics, culture methods, disinfection techniques for contaminated hatchery water for oysters, and the development of methodology for the culture of bay scallops and surf clams (Milford, Connecticut).

Total NMFS program funding for the marine aquaculture program is about $5.6 million (U.S.). NMFS also provided about $7.5 thousand to the states on a cost-sharing basis for marine aquaculture research and development activities under the Commercial Fisheries Research and Development Act of 1964 and the Anadromous Fish Conservation Act of 1965.

About 100 aquaculture projects are supported involving approximately $3.0 million in federal Sea Grant funds for scientists in 30 academic institutions. Major academic centers of Sea Grant-sponsored work on aquaculture exist in all coastal regions and the Great Lakes, as well as Alaska and Hawaii, with research generally focused on one or two species. Additionally, OSG contributes funding for aquaculture education, training, advisory/extension services, and planning activities

There is every reason to believe that aquaculture in the U.S. will expand, both in production levels and species cultured, over the next decade to meet the strong demand for high quality seafood that can be produced on a reliable basis. The degree and time-frame to which this becomes fact will depend upon successes by the industry in producing their product at a profit, plus the support of state and federal agencies in all areas of research and development as well as assistance with technology transfer and marketing activities.

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Table 1

United States Molluscan Shellfish Production, 1983

Species	Production (metric tons)[1]		Value ($U.S.)[4]
	Captured[2]	Cultured[3]	
Oysters (all species)	307,033	125,000	67,323,000
Clams			
Hard (M. mercenaria)	48,012	4,300	42,363,000
Surf (S. solidissima)	17,842	0	24,914,000
Mussels (M. edulis)	14,518	1,680	2,586,000
Scallops (all species)	185,072	0	136,322,000

[1] Live weight.

[2] Data are preliminary; NMFS, Wash., DC.

[3] Data are estimated; NMFS, Wash., DC.

[4] Captured value only; cultured value shown in Table 3.

Table 2

(From National Aquaculture Development Plan, Vol. 1)

U.S. Private Aquaculture Production[1] for 1980 and Preliminary Data for 1982

Species Groups	Value ($1000 U.S.)		Metric tons		Thousands of pounds		Percent of total	
	1980	1982	1980	1982	1980	1982	1980	1982
Baitfish	44,000	100,000	10,000	15,000	22,046	33,069[2]	10.7	8.4
Catfish	53,572	120,000	34,855	90,909	76,842	200,419[2]	37.2	50.7
Clams	10,398	12,000	1,777	2,045	3,917	4,508	1.9	1.1
Crawfish	12,951	27,000	10,849	25,000	23,917	55,115	11.6	13.9
Freshwater prawns	1,200	1,800	136	182	300	400[2]	0.1	0.1
Mussels	NA	1,600	NA	773	NA	1,700	-	0.4
Oysters	37,085	34,000	10,775	9,878	23,755	21,777	11.5	5.5
Pacific salmon	3,400[3]	4,000[3]	3,455	11,587	7,616[4]	25,544[4]	3.7	6.5
Tropical fish	NA	20,000	NA	NA	NA	NA	-	-
Trout	37,474	48,000	21,836	21,818	48,141	48,100	23.3	12.2
Other species[5]	NA	5,000	NA	2,273	NA	5,000	-	1.3
Total	200,080	373,400	93,683	179,465	206,533	395,632	100.0	100.0

[1] Data shown are live weight harvests for consumption, except for oysters, clams and mussels, which are meat weight. Excluded are eggs, fingerlings, etc., which are an intermediate product level.

[2] Projected estimated production for 1983.

[3] Pen-rearing only; ocean-ranching returns are currently used for brood stock.

[4] Includes pen-reared and ocean-ranched salmon.

[5] Includes such species as sturgeon, paddlefish, carp, buffalo, tilapia, mullet, abalone, etc.

Table 3

Estimated U.S. Private Aquaculture Production[1] for 1983[2]

Species Groups	Value ($1000 U.S.)	Weight (metric tons)
Baitfish	100,000	15,000
Catfish	132,000	100,000
Clams	9,500	4,300
Crawfish	30,000	27,300
Freshwater prawns	1,500	125
Mussels	1,500	1,680
Oysters	31,500	125,000
Pacific salmon	6,800[3,4]	9,400
Trout	50,000	22,000
Other species[5]	7,000	3,200
Total	369,800	308,005

[1] Data shown are live weight harvests including mollusks. Excluded are eggs, fingerlings, etc., which are an intermediate product level.

[2] Data are preliminary; NMFS, Wash., DC.

[3] Excludes the value of returning fish which were used for brood stock and were not sold.

[4] Includes pen-reared and ocean-ranched salmon.

[5] Includes such species as sturgeon, paddlefish, carp, tilapia, mullet, abalone, etc.

Table 4

Shellfish Seed Price List

Species	Price ($U.S.) Per Thousand*			
	2-3 mm	8-12 mm	12-16 mm	16-25 mm
Oysters				
Pacific (C. gigas)	$4.50	$12.00	$16.00	$22.00
American (C. virginica)	4.50	12.00	-	-
European (O. edulis)	4.50	12.00	16.00	22.00
Clam				
Hard (M. mercenaria)	10.00/9.00[1]	18.00[2]	25.00[2]	45.00[2]

* Prices based on minimum order of one million seed.

[1] Seasonal price difference for spring/fall delivery.

[2] Fall delivery only.

THE SELLFISH INDUSTRY IN FRANCE
(Economic importance, risks and constraints, research priorities)

M. BONNET *, J.P. TROADEC *

RESUME. La conchyliculture constitue en France une activité économique importante dont l'essor a débuté au milieu du siècle dernier. Elle occupe actuellement 24 000 ha du domaine public maritime et sa production dépasse 100 000 t pour l'huître creuse et 40 000 tonnes pour la moule,qui représentent une valeur de 1 300 millions de francs (1983). De plus, elle offre des potentialités de développement intéressantes, soit par la colonisation de nouveau espaces, notamment en eau profonde, soit en maîtrisant l'élevage de nouvelles espèces comme c'est le cas pour la palourde dont la production vient d'atteindre un niveau significatif (300 t en 1984).

L'ancienneté et le succès de ces élevages s'expliquent par les avantages importants qui découlent de la biologie et de l'écologie des mollusques filtreurs : alimentation sur une nourriture naturelle non utilisée par ailleurs, forte densité d'élevage, possibilité de captage de naissain naturel, sédentarité des espèces qui facilite le confinement des cheptels et l'aménagement des exploitations, l'attribution de la ressource se faisant par l'intermédiaire de l'allocation des sites (concessions).

Mais ces atouts s'accompagnent de points faibles dont peuvent résulter des périodes de crise aux sérieuses conséquences économiques et sociales :

- vulnérabilité particulière des mollusques, en raison de leur caractère filtreur et sédentaire, aux dégradations de la qualité du milieu marin (pollutions, eaux colorées).

- risques d'extermination des cheptels par des maladies épizootiques favorisées par la forte densité des élevages et les difficultés du contrôle dans un milieu fluide et ouvert,

- compétition pour la capacité trophique du milieu, naturelle et limitée, pouvant conduire à des excès de biomasse en élevage susceptible d'entraîner une baisse sensible des rendements et une plus grande vulnérabilité aux épizooties,

- concentration d'activités humaines de nature diverse (urbanisation, industrie, agriculture, tourisme) pouvant réduire la capacité biotique d'un environnement côtier très sollicité.

L'aménagement des bassins et des cheptels est un domaine prioritaire en France auquel s'attache la recherche, notamment par la conception de modèles de production conchylicole permettant d'estimer les biomasses correspondant à la productivité des sites d'élevage. Des études sont également développées en pathologie et en génétique pour minimiser les risques et les effets des épizooties et améliorer les performances des souches cultivées.

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* Institut Français de Recherche pour l'Exploitation de la Mer,
Direction des Ressources Vivantes, 66 avenue d'Iéna, 75116 **Paris**, France

ABSTRACT. Bivalve farming is in France a major economical activity, which development was initiated in the mid of last century. It occupies nowadays 24 000 ha of seabottom, leased from the French State, and production figures are above 100 000 tonnes for cupped oyster and 40 000 tonnes for mussel ; these made a gross value of 1 300 millions francs in 1983. Moreover, it shows potential for promising development, by expanding to new areas, especialy in deep sea, or by introducing new species, such as the short neck clam, which production has just reached significant level (300 T in 1984).

Long age and success of this cultivation activity come from the important advantages related to the biology and ecology of bivalves : food naturaly available, and of no use by another way, high density in culture, possibility of natural spat collection, sedentary nature enabling confinement of stocks and setting up of farms, resource allocation by means of leases.

But these strengthes are offset by specific weaknesses, which may lead to crisis situations, with serious economical and social consequences :
- specific vulnerability of bivalve molluscs, due to their filtering and sedentary features, and to the degradation of environment (pollution, red tides,...)
- risks of heavy mortality of stocks due to epizooties, enhanced by high density of stocks and difficulty of any control in an open water environment,
- competition for limited natural carrying capacity, resulting in overstocking, and then much slower growth and higher sensitivity to epizootics,
- increasing human activity of various types (urbanization, industries, agriculture, tourism) which may reduce the carrying capacity of coastal areas, highly demanded.

Planning has a high priority in France, and research is supporting it, noticeably for conceiving models of bivalve production, making possible biomass assesment in relation with productivity of culture sites. Researches are intensified in pathology and genetics to decrease the risks and consequences of epizootics and improve performances of cultured species.

I - INTRODUCTION

In France the practice of culturing molluscs goes back many hundreds of years. The first traces of mussel-farming appear in the 13th century (origins of the stick method), while culture of the European flat oyster began in the 17th century, when oysters were fattened in reservoirs in the salt marshes of the Atlantic coast. It was only in the mid-1900s, however, that this activity grew beyond the stage of simply harvesting natural beds.

This growth, which is particularly evident in the development of oyster farming, appears to have followed on three events which occurred between 1850 and 1870:

- mastery of the technique of trapping spat on collectors, whereas up to that time spat was harvested from natural beds,

- introduction of the cupped oyster, of Portuguese origin (*Crassostrea angulata)*, production of which grew very rapidly and far outstripped that of the native flat oyster *(Ostrea edulis)*,

- the first steps toward territorial development with the implementation of regulations governing exploitation of state-owned marine areas.

Figure 1 illustrates this spectacular growth in oyster production, which rose from some 10,000 tonnes in the early 1880s to 41,000 tonnes in 1911, 73,000 tonnes in 1930 and over 100,000 tonnes in 1953. It may also be seen that this growth was extremely irregular, with periods during which populations and production declined and collapsed being followed by sharp upswings for both the cupped and flat oyster.

Production collapses correspond to massive mortality due to epizootic diseases:

- for the flat oyster: epizootic disease in 1920/1927, *Marteilia* and *Bonamia*, which appeared successively in 1969 and 1979,

- for the Portuguese cupped oyster: branchial and viral infections in 1966/1973.

It is worth noting the repetition of this sequence: peak production moderate regression, appearance of one and often two epizootic diseases, collapse of production due to stock depletion. This could indicate that peaks may correspond to loads that are excessive in comparison with the carrying capacity of the shellfish ecosystem. Biomass excesses would cause a decline in production from existing stocks, along with the more serious problem of a decline in health status making the stock more vulnerable to pathogens.

A memorable drop in captures over two consecutive years (1934 and 1935) was responsible for production declines after these dates.

It is more difficult to interpret historical data with respect to mussels, since up until quite recently production statistics did not distinguish between quantities fished, which were quite large, and those resulting from culture. Analysis of these figures nevertheless shows that the increase in mussel production, which was particularly strong from 1970 on (Fig. 2), was also subject to fluctuations, although these were significantly less marked than in the case of oyster production. As opposed to oysters, mussels were not as heavily affected by parasitic diseases. As in the case of oysters, however, these fluctuations may have various causes. The production decline recorded in 1983 was due to two causes: a deficit in stock recruitment in mussel farms due to poor captures in 1982 and, to a lesser degree, prohibition of mussel harvesting and marketing during the summer because of toxicity due to contamination by the dinoflagellate *Dinophysis acuminata* (this mainly affected harvesting of natural beds).

In some areas, notably the Bay of Cancale, an increase in mussel loads led to significant production decreases, along with a rise in infestation by the parasite *Mytilicola intestinalis*. These phenomena have begun to regress since farm densities have been reduced.

This short history clearly shows that, although the shellfish industry has been a major economic development sector in France for almost a century, it has nevertheless experienced a succession of crises of varying degrees of seriousness, the dynamics of which have not been scientifically analysed. The task of determining and applying means for preventing or combatting these problems remains to be accomplished.

II - CURRENT ECONOMIC IMPORTANCE

Available statistics on the various components of shellfish production are not very reliable. Improvements in this area, presently under study by government, producers and researchers, will be determining factors in the development of shellfish culture and will have an even greater influence on planning with respect to stocks and basins.

The data available nevertheless has a relative value which makes it possible to perceive trends and identify periods of stability, separated by accidents or innovations. Evaluations made in recent years of the size and demographic composition of fishfarm biomasses have also shown that official statistics, when not closely linked to reality, most commonly underestimate actual production.

1 - Size of shellfish farms

Oyster and mussel farming has developed all along the Atlantic and Mediterranean coasts of France. These activities now cover a total area of nearly 24,000 ha, which may be divided into broad regions as follows:

Normandy - North Sea	=	1,500 ha
Brittany - Vendée	=	11,600 ha
Southwest Atlantic	=	7,600 ha
Mediterranean region	=	3,300 ha
TOTAL		24,000 ha

Most of this total is used for oyster-farming (approx. 20,000 ha), while mussel-farming, most of which is done on sticks, accounts for a total length

of 1,500 km of sticks, over an area of 1,600 ha. The total area also includes some 3,000 ha of deep-water seabed allocated over the past few years, mainly in the Gulf of Lions. This allocation corresponds to the recent extension of shellfish-raising activities into deep water, most of which is still in the experimental stage.

While fish-culture areas initially covered the most easily accessible strips of coastline (normally bare at low tide) and the most sheltered areas (coastal ponds, relatively closed bays), activities have gradually progressed seaward over the past 15 years due to lack of space on this strip, and in recent times have stretched into the open sea as deep as some 20 metres.

2 - Weight and value of production (Table 1)

Oysters

Oyster production has remained around 100,000 t since 1977, in spite of the fact that flat oyster production declined significantly as a result of epizootic disease. This decline has been compensated by growth in culture of the Japanese oyster *Crassostrea gigas*, particularly in Normandy and Brittany. In 1983, a good year for cupped oysters (109,100 t), turnover in the oyster-farming industry exceeded a billion francs (1,044.8 MF), notwithstanding low levels of flat oyster production (1,500 t).

Mussels

Cultivated mussel production has varied between 40,000 and 50,000 t over the past twelve years. In 1983, when below average tonnages were produced due to low spat-collection levels in 1982, sales were 210 million francs. On the average, mussel culture adds 10,000 to 30,000 per year to mussel yields from harvesting natural beds, although these latter vary from year to year due to fluctuations in the number of breeders. Combined fishing and culture yields reached a maximum of 80,400 t in 1981.

Clams

Culture of clams *(Ruditapes philippinarum)* has recently developed as a complement to traditional oyster and mussel farming. Production, though still experimental in many sectors, reached significant levels in 1984 with some 300 t, selling at 35-40 F/kg, for sales of at least 10 million francs.

3 - Number of facilities and employment

The great majority of shellfish farms have remained very small, often family enterprises, which would explain their large numbers (10,636 in 1983, although this is certainly overestimated). These enterprises total some 20,000 direct permanent jobs and an equal number of part-time jobs, most of which go to family members. These numbers may seem large in comparison with the value of shellfish production; however, apart from the family nature of these enterprises, which may involve accepting lower individual salaries (which may form satisfactory marginal gains with respect to family income), the profitability and wage levels of these enterprises should not be judged on the basis of sales of product alone. In addition to cultivation, the activities of these enterprises may also include packaging and marketing. This is the case for 3,500 of these operations, or a third of the total industry. Direct sales to customers are also developing in some production centres.

It would be interesting to determine whether the fact that the number of direct jobs generated in the shellfish-producing industry appears to be proportionally higher than that of the fishing industry means that the labour/capital ratio in the cost structure is higher in shellfish farming than in fishing.

Whatever the case may be, and in spite of the fact that statistical data is rather unsatisfactory, the shellfish industry occupies an important place in France's maritime economy, due both to the high production and many jobs it supports, and to the large areas involved. Insofar as sales are concerned, oysters are at the top of the list of all species fished and cultivated. In 1982, sales in the oyster-producing industry were 809 MF, followed by tuna fishing at 413 MF. Mussel and oyster farming combined represent, in weight and value, between a fifth and a quarter of national live resource production.

1979	Maritime fisheries	Shellfish farming
Weight	519,900 t (76.8%)	154,500 t (23.2%)
Value	3,034 MF (79.6)	778 MF (20.4%)

An evaluation of the socio-economic importance of the shellfish industry must also take into account its development potential. Better management of existing enterprises and extension into receptive areas would probably yield an increase in production in the order of 100,000 tonnes for mussels and 50,000 tonnes for oysters. As well, diversifying facilities by introducing new species with high sales values (e.g. Veneridae, Pectinidae) and providing better response to varying market requirements, could also yield considerable additional income.

These perspectives, although they are interesting given the deficit of our commercial balance for mussels and scallops, should not cause us to neglect the many risks and constraints (environmental, biological, technical, economic and social) already facing existing operations.

III - RISKS AND CONSTRAINTS

Among the natural and/or man-made risks liable to affect shellfish production, we have chosen to discuss the following:

- poor weather conditions (storms, extreme climatic conditions)
- chemical and bacterial pollution of urban, industrial or agricultural origin
- water discoloration phenomena, whether natural or brought on by some human activity
- epizootic diseases

Certain environmental changes may affect stocks and production by:

- low collection levels
- abnormally high mortality levels
- declines in growth and weight increase

Development of the shellfish industry is also facing various constraints:

- of a technical nature, although progress in this field with respect to material, equipment and automation, as well as in the biotechnical area (hatcheries) should allow these to be gradually eliminated,

- legal and political constraints, regarding conflict with other users of the coastal strip (tourist industry, fishing, industry, agriculture, urban development), as well as the means by which territory is allocated and granted,

- commercial and economic, in connection with organizing distribution and marketing, as well as promoting demand.

1 - Poor weather conditions

These may cause serious harm when extreme intensities are attained, which shellfish-farming facilities were not designed to withstand. Recent occurrences of this type, which reached disaster proportions, include:

- the severe storm which struck the Mediterranean coast in November 1982, causing heavy damage to 500 cultivation racks in the Thau pond (20% of shellfish-farming facilities), as well as the loss of 25% of oyster and mussel stocks,

- Cyclone Hortense, which struck the southwestern Atlantic coastline in October 1984, causing the destruction of part of the cultivation facilities and stocks in the Arcachon basin (losses estimated at 8,500 tonnes of oysters),

- to a lesser extent, the storm that raged over the Marennes-Oléron basin on November 15-16, 1984, resulting in the loss of nearly 3,000 tonnes of oysters.

In addition to storms, unusual variations in temperature cause problems. The period of exceptional cold early in the 1984-85 winter led to significant losses in cultivation facilities located in open areas. The same type of losses were recorded during the very severe winters of 1956 and 1963.

2 - Chemical and bacterial pollution

Preserving the quality of waters used for shellfish-farming is a critical matter, since this cultivation is practised in coastal areas with high population densities, particularly during the summer season, and significant industrializatior. Bivalves, being filter feeders, can concentrate high proportions of substances present in their environment. In France, half the coastline is urbanized or industrialized, and it is thus essential that attention be given to the problem of proximity of activites that might interfere with one another.

Pollution and changes due to human activity may have three types of effects:

- on productivity, i.e. stock yields,
- on stock mortality, including mortality in the larval stage,
- on the wholesomeness of products from a consumer standpoint.

In all cases, stocks are highly vulnerable, given the mixing of water through tidal action and the sedentary nature of seed.

Wholesomeness of shellfish is of particular importance in Franch, where these products are normally eaten raw, especially oysters. To protect public health, present regulations stipulate that culture may only be carried out in clean zones. Where exceptions are allowed on the basis of the production potential of areas showing a certain degree of bacterial pollution, producers are obliged to put shellfish from these areas through a purification treatment in special facilities normally using chlorine or ozone.

These regulations, which have led to the setting up of a country-wide inspection system, both of cultural environment quality and of product quality, have had the following main effects on enterprises:

- to increase costs, since producers must contribute to financing inspection activities (a peak of 2.85 million francs in 1983 represented the sale of 19 million inspection labels). In addition, some producers have been obliged to invest in storage and pre-treatment facilities to ensure the safety of their product (total investment of 600 MF for the 3,000 producers involved). Product cost must also include the cost of purification treatments (1 to 1.10 F/kg), although such treatment is basically required for imported shellfish.

- to inhibit certain development initiatives.

An example of the latter is Carteau Cove, in the Fos industrial zone near Marseille, where mussel-culture activites were limited by regulation to collection and nursery growth of spat, in spite of the fact that the carrying capacity of the environment also lent itself to the production of market-size mussels. Given the results of a recent study, which indicated that the risks of bacterial pollution were greater than those of chemical pollution, there are moves now to remove the prohibition on full cultivation, provided the mussels are only placed on sale after purification in approved facilities.

With respect to pollution that might affect seed productivity or cause abnormal mortality levels, government regulations state that shellfish farms may only be authorized in clean, protected zones. Among the extraordinary occurrences of pollution which have had a major effect on culture are:

- the sinking in 1977 of the AMOCO CADIZ, the cargo of which, in spreading over the coastline, caused the loss of a major proportion of the oyster seed in western Brittany. The damage this catastrophe caused to the shellfish industry has been estimated at 114 million francs, or a quarter of the total cost of the disaster (440 millions of francs in 1983).

- the second case had a less severe effect, but its economic and social impact was the same. This was pollution due to use of self-cleaning paints based on organostannous compounds which led to mortality in the larval stage and shell malformations in cupped oysters (thick flaky shell). The use of these paints was a major factor in the severe crises that struck oyster culture in the Arcachon basin, leading to low or nil

spat collections for five consecutive years and the temporary disappearance of half the fish-farming facilities. Demonstration of the harmful effects of these paints on the shellfish industry led to use of them being prohibited in France for treating the hulls of boats less than 25 m in length, which would be likely to travel through shellfish-raising areas (decree passed January 17, 1982).

On the whole, while there is a downward trend in the use of hydrocarbons, detergents and pesticides, certain highly exposed sectors are still recording rates of bacterial and chemical contamination that bear watching. It is also worthy of note that coastal municipalities have made sizeable investments in purification systems and plants.

3 - Water discoloration phenomena

Like pollution, to which they may be related insofar as their appearance may be partly an effect of inflows of nutrients, water discoloration phenomena vary as to origin, nature and effects. Whatever their diversity and complexity, however, these phenomena trigger two types of harmful effects when they develop in shellfish-bearing waters:

- fairly extensive mortality in biomasses under cultivation, resulting from the toxicity of plankton or anoxia of the environemnt,

- shellfish contamination by elements that are toxic to consumers, resulting in sales being prohibited.

Among the most noteworthy cases of mortality we may mention the "malaïgue" algae problem that occured in the Thau pool during the summers of 1982 and, particularly, 1975. This problem appears to be the result of the combined effects of a number of factors, in particular high temperatures, prolonged absence of wind causing water stratification, a high organic matter content, which set off a deterioration process leading to anoxia and the toxicity of the environment due to the presence of sulphurated hydrogen. In 1975, when the phenomenon spread to the entire basin, mortality amounted to nearly 70% of the stock (or approximately 15,000 to 20,000 tonnes of cultivated oysters and mussels), while in July 1982, when it was of lesser extent and shorter duration, some 10% of the cultivated biomass was destroyed.

Another case of extensive mortality, although of different origin, affected almost the entire stock of cultivated oysters and mussels in the Leucate pond in 1979-1980. In this case, the phenomenon took the form of an exceptional bloom of nannoplanktonic elements (chrysophyceae and chlorophyceae) which caused molluscs to lose weight and then die off.

With respect to problems resulting from contamination of shellfish products by planktonic elements containing biotoxins harmful to man, one case stands out due to the particular importance it has taken on in France in recent times. This is the phenomenon provoked by abnormal development of the dinoflagellate *Dinophysis acuminata* on the southern coast of Brittany and in some sectors in Normandy during two consecutive summers (1983 and 1984). This phenomenon, which necessitated setting up a specific monitoring system, led the government to pass measures prohibiting the sale of mussels from the areas affected. While hardships due to these prohibitions basically affected annual production, through a significant decline in quantities fished in natural beds, there were nevertheless some immediate repercussions on mussel

culture facilities. Apart from the temporary suspension of sales and the associated drop in income, these phenomena had a negative impact on the reputation of the product and caused some temporary disorganization in the market.

4 - Epizootic diseases

Epizootic diseases resulted in significant seed losses, mainly to oyster stocks. These diseases affected the various species as follows (Fig. 1):

Ostrea edulis:

- 1920-1927: heavy losses inflicted on stocks by a disease that has never been precisely identified.

- 1969 to date: appearance of marteiliosis, due to the parasite *Marteillia refringens*, followed by bonamiosis, in 1979, resulting from infestation of oysters by the protozoan *Bonamia ostreae*. These two diseases, which are still in evidence, caused considerable reductions in culture of flat oysters (10,000 to 20,000 tonnes between 1945 and 1960, and 1,300 tonnes in 1983).

Crassostrea angulata:

- 1966 to 1969: gill disease which rapidly spread to all cultivation centres and caused ever-increasing mortality.

- 1970 to 1973: viral disease causing extermination of all stocks, both wild and cultivated.

For the species *Crassostrea gigas*, which has been acclimatized in France and has made it possible to reconstitute total cupped oyster stocks very rapidly, there have been no occurrences of diseases of an infectious or parasitic nature that have had any noteworthy effect on production.

In the case of the two mussel species *Mytilus galloprovincialis* and *M. edulis*, both of which are cultivated, parasitic infections have never risen to serious epizootic proportions, although infestation by *Mytilicola intestinalis* can occasionally cause significant mortality. It should nevertheless be noted that the protozoan *Marteilia maurini* has recently shown a tendency to develop in mussels. Although the pathogenic action of this parasite has not yet been demonstrated, there is no assurance that it will remain benign.

Estimating the economic repercussions of epizootic diseases gives a good idea of their extent. A good example is that of the effects of marteiliosis and bonamiosis, which have contributed to the collapse of flat oyster production, particularly in Brittany, where this was a specialty. Although there has been a recovery in oyster culture using Japanese oysters as the flat variety declined, losses have been estimated at 1.6 billion francs (1983 value) for the period 1974-1982, or 180 million francs annually. To these losses may be added a reduction in value added in the order of 1.3 billion francs over the same period.

Comparison of these losses with those caused to the oyster industry of Brittany by the grounding of the Amoco Cadiz (114 million francs, 1983 value), but for one year only, shows the possible extent of the consequences of epizootic diseases. This result, reinforced by the memory of the recent extermination of the Portuguese oyster, has motivated those involved, professionals, government and the scientific community, to coordinate their efforts in order to better ensure the health status monitoring and preventive care of stocks. Measures taken to this end include:

- strict application of regulations prohibiting planting of imported shellfish in coastal waters,
- for imported shellfish intended for consumption, it is required to store these in approved facilities isolated from the marine environment and equipped with effluent treatment systems, should these shellfish not be placed on the market immediately,
- development of a system of health status monitoring of native stocks and imported products,
- reinforcement of research programs.

On the last point, start-up in the near future of an experimental establishment for mollusc pathology and genetics at La Tremblade should be mentioned. Although it may be expected that these research fields will yield interesting progress in the diagnosis of disease and development of prophylactic or therapeutic measures and the selection of stocks with better resistance to epizootic disease, work should also be directed to improving shellfish basin management. Given the genetic adaptation capacities of molluscs, which may well limit the prospects for manipulation of their genetic heritage, as well as the fluid nature of the environment, which reduces the possibility of prophylactic intervention, it is possible that in actual practice the most efficient approach will be that of preventive ecology, through regulation of stocks.

5 - Collection problems

From year to year, the various phases of the reproductive cycle, on which depends the success in collecting cultivation stocks, show different degrees of variation, which are normally due to variations in the natural conditions of the environment. Among factors causing variability, temperature plays a major role in acting chiefly on the triggering and progress of gametogensis and spawning and by regulating the abundance of planktonic food necessary both for breeding and for development of larvae.

The extent of these variations rarely reaches such extreme levels that there would be a deficit in collections. Throughout 47 years of cultivating *Crassostrea angulata* (1925 to 1972), there were only four years with no collection. For the species *C. gigas*, there were only two deficit years (1972 and 1981) in all the time it has been cultivated in France. In the case of stick-cultivated mussels, collection deficits occur on the average every 10 or 12 years, with the last dating back to 1982.

It may thus be considered that collection problems linked to natural conditions have not constituted a major constraint for the expansion of oyster and mussel farming in France, at least not unless these problems are encountered year after year, as was the exceptional case for cupped oysters in 1934 and 1935, following which years production did in fact decline conspicuously (Fig. 1).

These natural collection facilities hinder the development of hatcheries in spite of their recognized capabilities.

A man-made imbalance in the environment did, however, have disastrous consequences for collections. This involved the oyster *Crassostrea gigas* in the Arcachon basin where, for five consecutive years from 1977 to 1981, no spat was collected. Research undertaken to explain this anomaly showed that it was not a question of the capacity of breeders to produce viable larvae, but rather a problem of larval development. It was determined that veligers had failed to find the food they required in their environment. It was also shown that organometallic-salt based self-cleaning paints had a negative effect on larva survival, since they acted directly on the embryogensis process and the development of veligers, as well as interfering with production of the nanoplankton entering into their diet.

Prohibition of these self-cleaning paints coincided with the resumption of collection in the Arcachon basin, as well as with a marked decrease in anomalies of shell formation, providing further evidence of the toxicity of these paints for the larva and adult stages of oysters. Prohibition measures did, however, also coincide with other favourable events which are not necessarily linked to them. For example, improved yields (growth and fattening of oysters) appear to be linked with the noteworthy reduction in stocks present in the basin, due to a drop in collections. It has also been noted that the basin was recolonized by barnacles, which diminished the development of water plant communities and enriched the waters with their excrements, and this may have helped increase the productivity of shellfish farms. These considerations, notwithstanding their hypothetical nature, lead us to think that this prolonged lack of collection may not have been solely the result of the harmful effects of certain self-cleaning paints, but also of overloading of the basin. The dynamics of the crisis in the shellfish industry in the Arcachon basin are indeed complex.

It would seem that, while the use of toxic paints triggered the crisis, overloading due to competition between producers, along with poor chronology in the evolution of variables that were a determining factor in the regulation of the shellfish industry (carrying capacity of the basin, annual collection, biomass under cultivation, age profile of the stock, annual sales, etc.), also played a part.

6 - Abnormal mortality

During its cultivation cycle in France, the Japanese cupped oyster is subject to mortality rates that, although they vary with site and cultivation procedures, may attain and even exceed 30%. To these rates, which are considered normal, may be added additional losses that can reach very high figures. These abnormal mortality rates occur during the summer and, to a lesser extent, towards the end of the winter period. In both cases, they do not appear to be the result of infectious or parasitic diseases or environmental pollution.

Summer mortality was particularly alarming in 1981, when it affected the Arcachon basin and, particularly, in 1982, when it extended into the Marennes-Oléron basin while continuing to affect the Arcachon basin. From observations carried out in both areas, it appears that rising temperatures played a major role in triggering the phenomenon, which seems to correspond to a physiological imbalance following a period of intense metabolic activity and a significant deficit in carbohydrate reserves mobilized for sexual maturing. Young oysters are particularly vulnerable to this syndrome, which resembles that reported in Japan (Matsushima Bay) and the United States (State of Washington).

Winter mortality, which also affects young oysters, is apparently the result of fall conditions unfavourable to the development of sufficient energy reserves to last through the winter, during which period the production of plankton that forms part of the oysters' diet is very low.

These two types of abnormal mortality, although they differ as to environmental context (summer and winter), have a common factor, a deficiency in nutrition. It is possible that, given their physiological state at the time, the young oysters are unable to make the best use of the food available, but it is also possible that this food is insufficient due to excessive trophic competition following overloading. This hypothesis will have to be confirmed by studying the evolution of morbidity as a function of biomasses. If it does turn out to be correct, this will prove that mortality among the youngest individuals acts as population-regulating phenomenon that depends on the capacity of cultivation sites.

7 - Problems of growth and fattening

Notwithstanding seasonal variations, the growth rates and quality of oysters and mussels show abnormal reductions from one year to another that have an impact on yield levels and selling prices, and thus on the profitability of enterprises.

These growth and fattening problems are sometimes caused by climate conditions which, although natural, are abnormal, leading to a significant decline in the productivity of the shellfish industry. In the Thau pond, for instance, a drop in fresh water supply during drought years was cited to explain the poor quality of mussels observed during that time. The undernourished state of oysters may also correspond to temporary temperature deficits that caused a decline or a delay in phytoplankton production.

These problems often appear to be caused or aggravated by overloading of cultivated biomasses with respect to the carrying capacity of the system. Risks of imbalance would obviously be higher in semi-closed sites (basins or ponds), where food supply replacement through water replacement is limited, than in more open environments (currents, upwelling).

While noticeable declines in yields observed in various sectors appear to be chiefly due to biomass excesses, we do not at this time have sufficient knowledge of the productivity of shellfish-raising environments and the energy requirements of molluscs to be able to verify this hypothesis, nor to develop models that would enable us to determine the appropriate loads for various basins.

Development of research on the ecology and productivity of shellfish basins is thus a priority. Basically, this research would proceed along two main lines:

- an empirical approach, aimed at determining the relationships between annual production, length of the growth cycle and morbidity on the one hand and the biomasses of existing stocks on the other,

- an analytical approach destined to evaluate the trophic requirements of shellfish stocks and their competitors, as well as the nutritional capacity of basins, and to compare these requirements and this capacity.

These two approaches are complementary, the first being likely to lead rapidly to decision-making guidelines for each basin, although it remains less heuristic than the second. The empirical approach may also yield strong signals, the nature and origin of which may then be analysed using the second method.

This question is also complicated by variations in climate and hydrology from one year to another, as well as by anthropic changes in the productivity of basins (changes in fresh water supply from rivers, increased sedimentation due to shellfish cultivation, etc.).

These research areas have developed in the Marennes-Oléron basin with the expectation that methods and models developed in other shellfish-raising centres throughout the country will also be implemented there. In this basin, which ranks first among all the oyster-raising centres of Europe by its production levels, the low yields observed over the past two or three years have given rise to two hypotheses. The first suggests that existing stocks exceed the basin's carrying capacity. The second, based on the fact that these biomasses are apparently not greater than they were in the past, suggests a decline in the productivity of the basin. This decline could have two causes: rising bottom levels due to significant sedimentation leading to a decrease in flows distributing food to the molluscs, or a drop in the inflow of nutrients which might result from increase use of the waters of the Charente River upstream by agriculture and urban centres. These two hypotheses must be tested and their respective effects evaluated if possible. A mathematical model allowing the physical and biological parameters of the basin to be integrated is currently being developed.

8 - Technical and biotechnical problems

The fact that shellfish enterprises are often old and small-scale does not mean that they have not benefitted from technological progress. Over the past fifteen or twenty years, the floating equipment used (amphibious barges, hydraulic cranes for collecting mussels on sticks, etc.) has been modernized and better adapted to the industry. As well, in certain regions where this has been feasible, for instance in Normandy, use of farm tractors has become a general practice. Use of new materials for collection and cultivation structures (plastic collection devices and scoops, aluminum racks and sticks, etc.) has also contributed to progress, as has the use of machinery for packaging (conveyor belts, sorting belts, etc.). As well, in the biotechnical area, recent mastery of techniques for producing spat in hatcheries and nursery culture and maturation processes for clams has opened

up an interesting avenue for diversification, which is now moving into the development phase. Gaining control over reproduction also means that it may be possible to manipulate the genetic heritage of stocks.

There are nevertheless gaps which may detract from the yield of existing enterprises or act as a hindrance to full development of this potential, whether it be the extension to new sites or promoting the raising of new species.

For existing facilities, there is a particular need for progress in collection operations, detachment procedures, sorting and packing oysters, all of which could benefit from greater mechanization.

Extension of cultivation into new sites mainly involves moving into deeper, open waters; this is where the greatest potential lies, since the sheltered coastal areas are now practically all covered. The various attempts to move into open waters, particularly over the past ten years in the Mediterranean, have brought to light the difficulties encountered in developing cultivation structures able to resist poor weather conditions at acceptable investment and operating costs. These attempts, mainly involving mussel-farming on strings, have nevertheless confirmed the fact that in many sectors, and up to depths of 20/25 m, the waters provide good yields, as regards both quality and quantity of product. Provided the current industry and research efforts result in economically and technically viable solutions, there are interesting prospects for extension of the shellfish industry into open waters in France.

Diversification of production processes through mastering techniques of raising new species may also have several advantages: better utilization of sites by taking advantage of the complementary behaviour of molluscs, particularly on a trophic level; source of additional income, making for better profitability; better response to market demand; a decrease in the risk of epizootic diseases, which is always higher in monoculture situations. Successful cultivation of clams is an accomplishment in this area, made possible by mastering the technique of hatchery reproduction. For other species, such as scallops, of which production of natural stocks is insufficient in France, research and development activities are being directed by a different strategy:

- first, to reconstitute natural stocks from hatchery spat, in order to be able to make collections from these stocks of natural spat for cultivation (since the cost of hatchery spat at the present time is prohibitive),

- second, to find an explanation of the mechanisms that govern successful breeding in natural circumstances, in order to better perceive the possibility for forcing natural selection and to determine the best seeding methods (age of spat, time and space parameters for release, quality of spat, etc.).

9 - Competition for space

The large areas of state-owned marine space allocated to the shellfish industry (24,000 ha) gives an idea of the dominance this activity has achieved over the coastline. It is certain, however, that access to favourable sites

is becoming difficult, since they are becoming increasingly rare, due both to the development of shellfish-farming operations themselves and to increased pressure from other coastal activities (agriculture, industry, urban growth, tourism, etc.). On examination, it may be seen that the main difficulties encountered by spatial expension of the shellfish industry are due to:

- choices with respect to development policy: This is the case, for example, when the authorities responsible for planning in coastal areas decide to develop other areas of activity that are judged incompatible with aquaculture. Some municipalities have been reluctant to allow the shellfish industry to operate on their territory, preferring to save the land for tourist development which would yield more income to them. One reason for this attitude is certainly the fact that, due to the legal status of state-owned coastal land, there is little financial benefit for municipalities.

- technical incompability: This occurs when the cleanliness of the areas in question does not satisfy the requirements of current legislation. An example is the bay of Fos, where industrialization has created an obstacle to development of mussel culture. A similar situation is encountered when cultivation loads have already reached levels which it would not be wise to exceed. An example is the Marennes-Oléron basin, where it was decided only to grant concessions for clam cultivation where these would be substituted for concessions already used for oyster culture, and only for a period of two years, in order to be able to evaluate the profitability of yields in this area that is already in intensive use.

- diverging interests within the marine industry. One of the most noteworthy cases of this type of situation is that opposing the extension of shellfish-raising facilities into open waters to trawling activities in the Gulf of Lions in the Mediterranean. There are already conflicts over development of clam cultivation on the foreshore which, in some sectors, has brought protests from shore fishermen and others who have traditionally had access to these areas and their natural resources. There is also a certain amount of opposition on the part of established shellfish-farmers towards development projects by agents outside their industry (fishermen or independents) or from outside their region.

More generally, development of the shellfish industry will depend on:

- the terms for granting and trading concessions,

- preparation and adoption of basin development plans (structural plans)

Basically, transfers of concessions might be made in two manners:

- on the basis of decisions based on legally defined criteria such as membership in a professional body (registered marine workers) or proof of specific qualifications or experience,

- through the use of economic mechanisms.

While the first method introduces rigidities and inequalities into conditions for access and may cause the authorities responsible for making the

concessions to be subjected to strong pressures, the second may seem somewhat surprising given the tradition of free access to state-owned marine territory. Because of these traditions and the necessity of combining private interests at the enterprise level with administration of state-owned lands (development of shellfish basins and stocks, administation of the many uses made of marine territory, etc.), it may be expected that changes in this area will be gradual.

Preparation, through cooperation between the shellfish industry and the appropriate authorities, of basin development plans (choice of appropriate crops, distribution of these among industry members, deciding on optimum geographical distribution of cultivation centres, etc.) will be facilitated through the appropriate studies and scientific consultation. From this standpoint, developing shellfish production models for basins facing overloading problems is a priority.

10 - Market organization

French eating habits mean that many shellfish are eaten raw. This is almost always the case for oysters. This leads to certain constraints in market organization with respect to packaging and sale of a live product, which is additionally stored outside its natural environment, as well as the sanitary quality of this food product, which must be maintained from the time it is harvested until it is eaten. These habits also mean, in the case of oysters, that a large part of the production is consumed during the Christmas and New Year's period. In 1982, for example, 65% of sales took place during the fourth quarter, and 51% during the month of December alone. This markedly seasonal nature of sales in the oyster industry only servesto complicate organization of the market, as does the practice of direct sales from producer to consumer, which is on the rise at the present time. All of these factors might lead one to believe that the current level of production of 100,000 t of oysters corresponds to the maximum the domestic market can absorb, whereas it is likely that better organization of this market, along with more emphasis on export potential, could on the contrary justify additional production efforts.

The situation is different in the case of mussels. As opposed to the oyster, mussel consumption is spread throughout the year. The fact that quantities available are clearly insufficient, combined with seasonal drops in the quality of French production, have led to establishment of an import market which may supply up to 50% of the French market (in 1983, France imported 42,500 t of mussels, valued at 117 million francs). The size of this production gap is an encouragement to the development of domestic production of mussels, which is currently underway in several regions and in particular through introduction of cultivation structures in open and deep waters. It should, however, be noted that anticipated production gains will not necessarily stop the inflow of imported mussels, if only because the top-market quality of French production will not necessarily be in competition with low-cost imported products.

These considerations demonstrate the interest of carrying out market studies that would provide an objective estimate of the capacity of the domestic and export markets, in order to better organize marketing and make decisions on goals and the desirability of various development plans.

IV - CONCLUSIONS

Both in France and on a world scale, the shellfish industry is a clear leader in the cultivation of sea animals (3.2 million tonnes, FAO 1983). This remarkable progress may be explained by the combination of several strategic advantages of bivalves for development of marine coastal areas:

- frequent possibilities for collecting natural spat,
- diet based on otherwise-wasted natural food,
- bivalves are filter-feeders, thus allowing high cultivation densities,
- sedentary nature of molluscs, which facilitates both confinement of stocks and the disposition of facilities, both of which may be decided on to a great extent by operators, while resource attribution is effected through site allocation (concessions).

But there is another side to these advantages. In spite of the remarkable progress in the shellfish industry, there are periodic crises, in particular involving epizootic diseases, which have serious economic and social consequences. Disease is not the only problem; the crisis in the Arcachon basin, when over a five-year period no spat was collected, emphasized the need to ensure that water quality is maintained at adequate levels. It is thought that this absence of spat was due to the use of self-cleaning paints on the hulls of pleasure and working vessels.

Analysis of these crises reveals another underlying problem, even more critical for the development and improvement of this type of cultivation: the tendency of shellfish-farmers to load basins beyond their carrying capacity. This may be the result of competition between operators for an ecosystem that is limited by natural causes but not formally partitioned out to operators. In these conditions, the only option operators have is to increase their stocks in order to attempt to capture an ever-increasing share of this limited production capacity and the profits attached to it, or simply to prevent their share from decreasing as other operators' stocks increase. This hypothesis suggests that shellfish resources could in practice be only partially allocated by granting concessions, and that the knotty problems of developing and using common resources, of which the best documented example is probably the fishing industry, also affect the shellfish industry whenever operations reach a certain degree of intensity. If the practice of overstocking and the motivations for doing so are confirmed, then the question of regulating biomasses and the terms for granting and trasferring individual territories will have to be faced. This problem will nevertheless only become acute in basins which are not sufficiently open and which are overworked, where the trophic demands of biomasses under cultivation are likely to exceed the carrying capacity of basins. This may not be the case for all areas.

This conclusion, presented as a hypothesis, should not be too surprising. It may be compared to the natural tendency of the shellfish industry to expand. There may be objections to this judgement with regard to a type of culture where biomasses may be as dense as 100 t/ha (horizontal culture) or even 200 t/ha (suspended culture). Nevertheless, in terms of means of exploiting ecosystems, we are certainly dealing with an extension-prone form of culture, insofar as human intervention is limited to seeding natural ecosystems in order

to manipulate its specific quantitative composition to increase production. Initially, there is no need to add food nor to physically change the environment. It is only in the more sophisticated forms of culture (e.g. cockle-farming) that spat must be produced artificially and there is an early maturing period in a more or less controlled environment.

In these conditions, it is not surprising that planning development of basins and shellfish stocks appears as the major problem facing this activity in the future, as well as being a research priority. There are a number of aspects to this problem:

- determining the trophic requirements, both quantitative and qualitative (nature of plankton forage, species, particle size), of cultivated species and their competitors,

- evaluating the productivity of basins and probably of their major variations, both from season to season and from year to year, since deficiencies may occasionally appear,

- designing and applying shellfish-culture models to enable an estimate to be made of biomasses corresponding to basin productivity and, if possible, how production may vary according to loading,

- development for each individual basin of empirical models based on historical statistics linking production, duration of cultivation cycles and morbidity of existing biomasses,

- preserving the quality of waters used for shellfish-raising along with their trophic capacity with a view to eventually being able to manipulate this capacity in semi-closed basins by varying fresh water supply and nutrient loads (purification),

- analysis, based on shellfish-raising models, of the economic and social consequences of various loading levels in order to compare the various planning goals for a given basin,

- development of regulatory methods that would facilitate the application of the development plans chosen, insofar as these methods would enable individual and collective interests to better coincide (systems for allocating and transferring concessions, biomass sharing within the limits adopted, etc.).

Applying the results of this research implies implementation of a statistics program that can evaluate and track the main variables that affect the state of shellfish stocks, in particular those which may be varied in order to achieve the most efficient operation within a given set of parameters: total area and geographic distribution of concessions, biomass and composition of stocks (species, demographic structure), as well as of competitors, cultural techniques used, production and transfers (weight and demographic structure), collection of spawn, etc. Variations from year to year of some of these variables should be recorded, since the system will be subject to external hazards (natural variability of the environment and of collections, as well as market fluctuations) which it would be useful to be able to predict and, if possible, to regulate.

This type of planning and the research behind it will be necessary and justified in basins that are heavily farmed and relatively closed. As with any development work, success will necessitate close cooperation between industry, administration and research, involving cooperation for the collection of statistics essential to the collective administration of the use of resources held partially in common, cooperation for the analysis and choice of possible development objectives and the preparation and application of appropriate development plans.

In spite of the difficulties involved in therapeutic action on a liquid environment, pathological studies are important for several reasons: to monitor the health status of the environment and take the appropriate prophylactic measures (prohibition of transfers, for example), to determine standards (e.g. densities) and cultural practices (cultivation cycle as compared to the production cycle and that of disease transmission) most likely to minimize the risk of epizootic disease.

Genetics is another discipline which holds out much hope for reducing the effects of disease and improving the zootechnical performance of stocks. The prospects offered by genetic manipulation for the selection of disease-resistent stock, or stock that would provide better yields, will depend on the ability of molluscs to maintain a differentiated genetic heritage.

The other avenue for compensating for the limits of natural basin productivity consists in introducing new species, as well as domesticating other species likely to contribute to more complete use of this productive capacity and to reduce the inconvenient aspects of monoculture, both with respect to cultivation (incidence of epizootic disease) and to marketing. Mastering new species will depend mainly on progress in aquaculture technology (culture on strings or other structures in deep waters). Progress has already been made in this direction. The same is true of diversification: recent domestication of the clam to the point of economic viability, the successful domestication of the scallop in Japan or progress made in France towards mastering the latter species are all only the initial steps toward greater diversification of the shellfish industry. Development of intensive shellfish cultivation will be greatly assisted by progress in determining how marine populations should be chosen. This progress will be of vital importance in selecting species and defining release procedures that will make it possible to encourage natural breeding and production.

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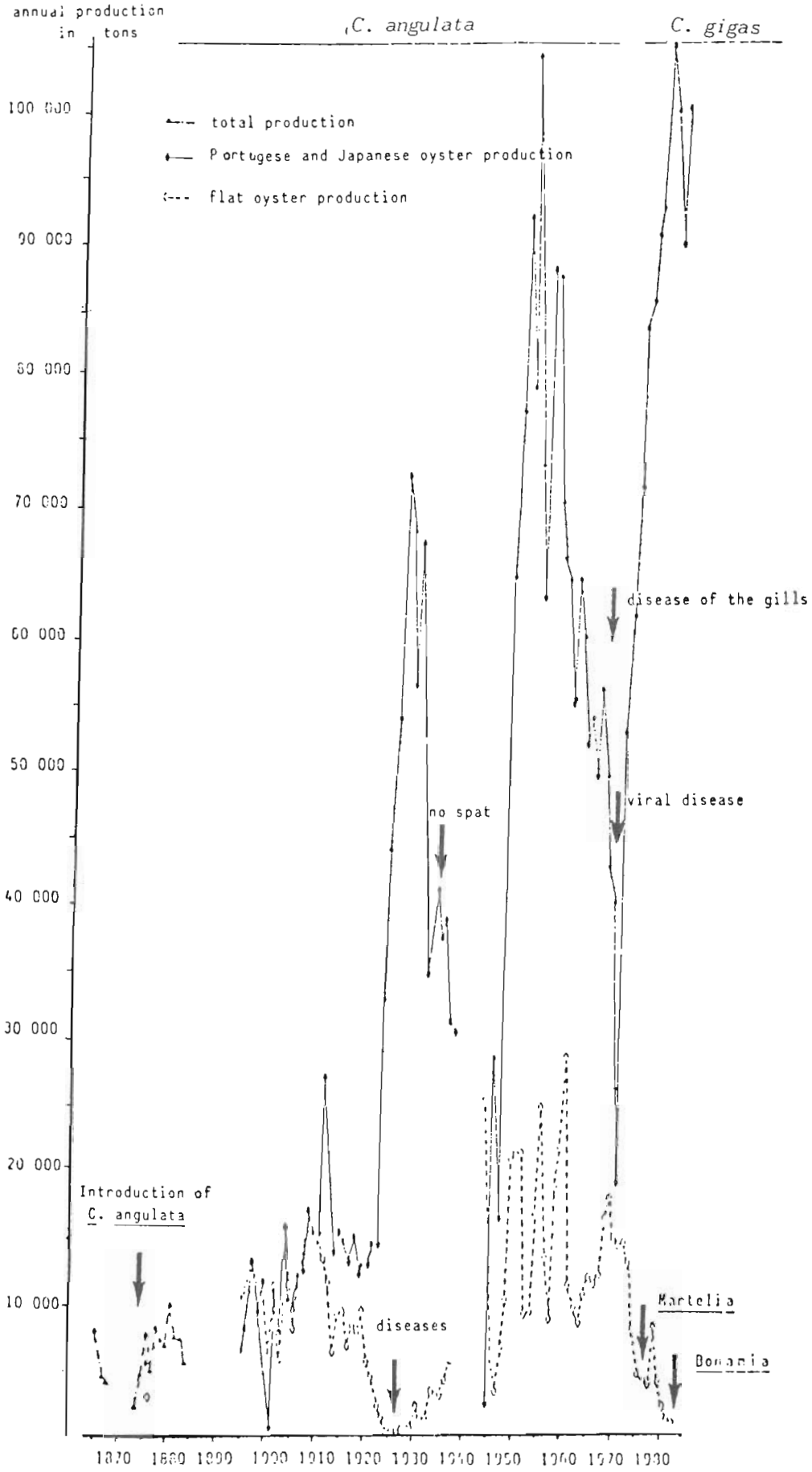

Figure 1 : Evolution of the oyster production in France from 1865 to 1983. From Héral, 1985.

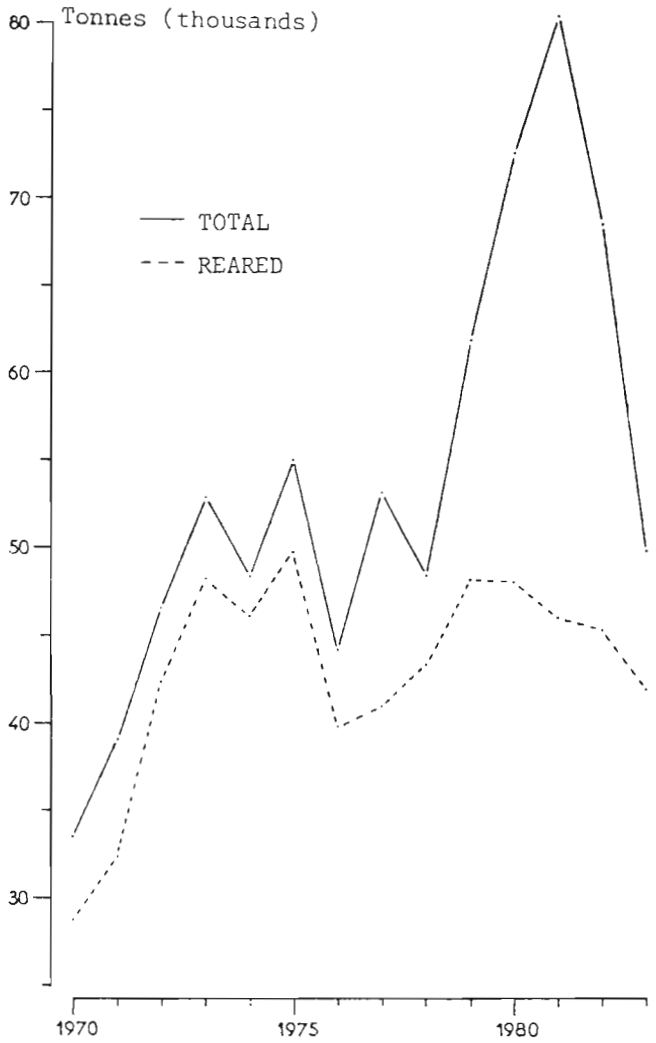

Figure 2 : FRENCH MUSSEL PRODUCTION FROM 1970

Species \ Years	1977	1978	1979	1980	1981	1982	1983
Cupped oyster							
C.angulata							
Weight	96 600	91 700	100 300	95 200	82 800	87 200	109 100
Value	505 850	530 800	541 600	653 800	579 500	767 400	1 016 800
Flat oyster							
O.edulis							
Weight	3 800	3 600	6 000	4 200	2 800	2 600	1 300
Value	59 000	63 300	91 000	83 150	40 700	42 100	28 000
Total oysters							
Weight	100 400	95 300	106 300	99 400	85 600	89 800	110 400
Value	564 850	594 100	632 600	736 950	620 200	809 500	1 044 800
Mussel							
Weight	40 950	43 500	48 200	48 150	46 100	45 350	42 000
Value	123 000	130 300	145 000	193 000	184 200	204 000	210 000
TOTAL							
Weight	141 350	138 800	154 500	147 550	131 700	135 150	152 400
Value	687 850	724 400	777 600	929 950	804 400	1 013 500	1 254 800

Table 1 : bivalve farming production from 1977 to 1983, by weight (tonnes) et value (french Francs).
Are not included landings from wild stocks.

SHELLFISH CULTIVATION IN THE UNITED KINGDOM

C.E. PURDOM *

RESUME. La conchyliculture en Grande-Bretagne est d'un tonnage réduit. La détermination de sa production exacte est rendue impossible par l'absence de distinction dans les statistiques entre produits de la pêche et d'élevage.

Seules les huîtres et les moules sont élevées. La majeure partie des 300 à 600 tonnes d'huîtres mises en vente annuellement provient d'élevage. Inversement les moules d'élevage ne représentent qu'une faible part des 6000 tonnes commercialisées annuellement.

Les méthodes d'élevage sont simples et traditionnelles ; mais,pour l'élevage larvaire et la nourricerie,des méthodes sophistiquées sont mises en oeuvre.

Les potentialités des côtes de Grande-Bretagne sont sous-employées. Mais la demande nationale pour les coquillages est très faible ; elle pourrait être remontée à un niveau similaire à celui de la fin du XIXème siècle grâce à une promotion commerciale dynamique. Mais,de par leur faible nombre et de leur taille réduite, les entreprises d'élevage ne peuvent prendre en charge celle-ci.

Hormis Ostrea edulis et Crassostrea gigas, couramment élevées, les espèces faisant l'objet d'étude en écloserie sont : O.Lutaria, C.Virginica, Venus decussata, V.semi-decussata, Mercenaria mercenaria et Haliotis rufescens.

Landings of shellfish at British ports are not classifed according to origin so the amounts deriving from cultivation cannot be assessed. The mollusc landings for the UK are listed for 1979-1983, in Tables 1 + 2 together with first sale values. Landings of scallops, cockles, mussles and clams are almost all from wild stocks, some of the mussel and most of the oyster landings derive from managed or cultured beds. Following dredging from natural stocks, there is reason to believe that the oyster landings, in particular, are serious underestimates.

Oyster landings are not classified by species but most of the records refer to native oysters O.edulis with a seasonal harvest during winter. Pacific oysters, C.gigas are harvested in small quantities throughout the year. Recorded landings have been reasonably contant at about 600 tonnes/year but this is very low compared to peak landings of about 3000 tonnes/year in the Nineteenth Century and lower still in relation to the available oyster grounds which could support many thousands of tonnes.

Mussel landings are around 6,000 tonnes/year and as for oysters, potential yields are very much greater than this. Clam landings mostly come from an apportunistic fishery for hard-shelled clams (M.mercenaria) in Southampton Water but the fishery appears to be in steep decline, after a 1981 peak of 1500 tonnes, due to failure of recruitment.

The cultivation/harvesting of all of these molluscs is basically by fairly primitive methods involving ground laying. Some raft developpments have taken place in Scotland (and Ireland) for mussels but a serious limitation on UK shellfish farming remains its lack of expansion into all three dimensions of the water mass.

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* M.A.F.F. Fisheries Laboratory, **Lowestoft**, Suffolk, Great-Britain

Highly sophisticated hatchery techniques and some advanced upwelling systems with or without managed lagoon facilities are operated for the spat and nursery phases of growth, respectively, but the final grow-out stages are still conducted along traditional lines.

The potential for culturing for molluscs around the UK coastal is very high. Suitable localities can be identified in almost every sector of the coastline and overall there may be as much as 15,000 hectares of good quality ground.

Although the potential exists for large-scale molluscs production in England and Wales, actual production falls far short of potential. Some areas suffer from sewerage pollution, but there are well established low cost procedures to overcome this problem. There are some pests and diseases of shellfish which make restriction of movements necessary to prevent spread of the pests ; but these are unlikely to restrict production. There are local conflicts on use of the coastal zone, but again these usually affect only a very small area. It must therefore be concluded that a lack of home markets is the main constraint on UK shellfish production. Although, to take on example, about 4,000 tons per year of oysters were consumed in the UK up to the first world war landings declined seriously at about that time due to various factors. The price of oysters increased and many people stopped eating oysters and turned to other foods. It is now two generations since oyster eating was widespread ; in that time many other foods have come onto the market to fill the gap left by oysters.

Wherever oysters have recently been produced in quantity and marketed with vigour they have sold well.

Probably the market for other shellfish could be improved with a marketing campaign, but with a limited number of producers growing on a small scale, they would not fund such a campaign, nor could they respond to demand if it was successful.

The best that can be expected is that the rabit of shellfish eating will spread gradually, and that production will rise to meet the demand.

Research designed to increase shellfish cultivation comprises studies of hatchery methods, nursery techniques and on-growing strategies for those species for which full culture practice is possible. For species dependent on natural spatfall, scallops and mussels, spat collection is the major field of enquiry together with subsequent husbandry technique.

A wide range of bivalve species can now handled in hatcheries although for all of them except perhaps C.gigas, some reliance is still placed on intuitive technique and this cannot always be relied on. The species studied in the UK include, in addition to C.gigas, O.edulis, O.lutaria and C.virginica amongst oysters, and V.decussata, V.semi-decussata and M.mercenaria - the clams and H.rufescens, the abalone. Hatchery study basically comprises definition of spawning techniques, spat collection and the provision of feeds.

Nursery studies include the development of pumped and tidal upwelling systems with or without managed lagoons, and the establishment of crab proof fences or the use of protective cages of other sorts. For ongrowing studies, trial plantings of molluscs are carried out at selected sites to assess growth and survival. Increasing attention is being placed on the possible laying of native oysters and some clams so that natural reproduction and spatfall can occur before harvesting.

Disease control is monitored primarily at the MAFF Fish Diseases Laboratory under Control of Deposit legislation but Public Heatlth responsibilities reside with the Aquatic Environnement Pollution Section 2.

TABLE 1. LANDINGS (TONNES) OF MOLLUSCAN SHELLFISH IN THE UK 1979-1983

1979

	England and Wales	Scotland	Northern Ireland	UK
Oysters	664	-	-	664
Mussels	4691	819	-	5510
Cockles	10415	..	-	10415
Queens	1414	4712	43	6169
Scallops	3566	3710	67	7343
Winkles	157	2865	207	3229
Whelks	1759	26	-	1785

1980

	England and Wales	Scotland	Northern Ireland	UK
Oysters	595	-	-	595
Mussels	8619	526	-	9145
Cockles	15242	-	-	15242
Queens	1239	5020	..	6259
Scallops	3222	5320	41	8583
Winkles	116	2725	393	3234
Whelks	1209	26	-	1235

1981

	England and Wales	Scotland	Northern Ireland	UK
Oysters	577	-	-	577
Mussels	2369	146	-	2515
Cockles	10438	10	-	10448
Queens	2952	5684	..	8636
Scallops	3026	5521	33	8580
Winkles	116	2710	102	2928
Whelks	1494	9	-	1503

1982

	England and Wales	Scotland	Northern Ireland	UK
Oysters	417	..	-	417
Mussels	4388	50	-	4430
Cockles	8300	..	-	8300
Queens	2094	3699	-	5793
Scallops	2348	6533	13	8894
Winkles	134	2337	276	2747
Whelks	1642	1	-	1643

1983

	England and Wales	Scotland	Northern Ireland	UK
Oysters	290	..	-	290
Mussels	5823	33	-	5856
Cockles	5836	1	-	5837
Queens	4206	4433	8	8617
Scallops	2749	5090	3	7842
Winkles	138	2402	224	2764
Whelks	1344	2	-	1346

The sign.. indicates a quantity of less than 0.5 tonnes or a value less than 500 according to the table.

TABLE 2. VALUES (£000) OF MOLLUSCAN SHELLFISH LANDED IN THE UK 1979-1983

1979

	England and Wales	Scotland	Nothern Ireland	UK
Oysters	1009	-	-	1009
Mussels	237	34	-	271
Cockles	504	-	-	504
Queens	270	1045	20	1335
Scallops	1605	2210	46	3861
Winkles	31	671	45	747
Whelks	257	4	-	261

1980

	England and Wales	Scotland	Nothern Ireland	UK
Oysters	1001	-	-	1001
Mussels	428	32	-	460
Cockles	807	-	-	807
Queens	256	1123	..	1379
Scallops	2235	3288	14	5537
Winkles	28	718	55	801
Whelks	255	4	-	259

1981

	England and Wales	Scotland	Nothern Ireland	UK
Oysters	1116	-	-	1116
Mussels	211	18	-	229
Cockles	591	2	-	592
Queens	640	1293	-	1933
Scallops	2060	3253	61	5374
Winkles	25	739	23	787
Whelks	350	1	-	351

1982

	England and Wales	Scotland	Northern Ireland	UK
Oysters	925	..	-	925
Mussels	453	8	-	461
Cockles	458	..	-	458
Queens	463	828	-	1291
Scallops	1623	4171	36	5830
Winkles	37	680	58	775
Whelks	380	..	-	380

1983

	England and Wales	Scotland	Northern Ireland	UK
Oysters	636	..	-	636
Mussels	461	7	-	468
Cockles	327	..	-	327
Queens	955	1133	4	2092
Scallops	2351	3763	6	6120
Winkles	36	770	58	864
Whelks	225	0.7	-	225.7

The sign.. indicates a quantity of less than 0.5 tonnes or a value less than 500 according to the table.

GENERAL OVERVIEW ON BIVALVE SHELLFISH FARMING IN ITALY

P. BREBER *

RESUME. Activité datant de l'antiquité, la conchyliculture en Italie a connu une évolution il y a une trentaine d'années. La moule a presque totalement pris la place de l'huître. La production annuelle est d'environ 100.000 t. Les zones de production sont dispersées tout le long des côtes italiennes, dans les lagunes et baies peu profondes.

La méthode traditionnelle d'élevage en suspension a connu récemment deux améliorations importantes : le remplacement des cordes végétales par des filets et l'utilisation de filières flottantes qui permettent l'implantation de fermes en mer ouverte.

Les résultats de la recherche sur l'élevage de l'huître n'ont pas encore interessé les producteurs ; par contre,ceux sur la palourde les ont beaucoup motivés.

La pollution des eaux a des conséquences très néfastes en obligeant à fermer certaines zones à l'élevage et à pratiquer une épuration coûteuse des coquillages provenant de certaines autres.

Bivalve shellfish farming has been practiced since Antiquity Renown places according to ancient authors were Brindisi and Lucrino near Napoli. On the 16th Century this activity has been moved from Lucrino lagoon to Nearby Fusaro lagoon ; it received privilege of the protectorate of King of Napoli. On eastern coast, Tarente took preeminence over Brindisi, and bivalve shellfish farming became a privileged activity. A multisecular tradition of oyster farming also exists in the Venice lagoon.

Oyster (Ostrea sp.) was the most common species of bivalve raised since thirty years ago. Trieste, Venice, Brindisi, Napoli and La Spezia were the production centers. But today oysters have almost disappeared, being replaced by mussels.

Mussel production in Italy is estimated at 100.000 tonnes, increasing. Mussels are marketed alive. Gulf of Trieste, Grado lagoon, Venice lagoon within Po delta area mainly lagoons of Caleri Scardovari, and Goro, Ravenna, Cattolica, Ancona, gulf of Manfredonia, Mare Grande of Tarente, gulf of Napoli, gulf of Gaeta, Paola lagoon, gulf of La Spezia, gulf of Olbia, Muravera lagoon are mussel farming areas.

Rearing technic is mostly the Tarente one, with slight modifications : poles planted in the mud, in shallow waters, support a framework made of horizontal cables, on which are hanged of mussels. A recent and important improvement has been use of sock net, in place of vegetal rope (Spartina sp.)
Another very interesting and more recent improvement has been substitution of planted poles by buoys, which made possible to occupy deeper and less protected waters. Consequences of this new technology can be seen on considering the huge number of these structures occupying open sea in the gulf of Trieste.

A totally different way is followed in Goro lagoon, where bottom culture, in a simple manner, is practiced, as in the Netherlands.

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* Instituto - C.N.R., Via Fraccarcreta 1, 71010 **Lesina**, Italie

Research in Italy, supporting bivalve shellfish farming, tends to drive it out of monospecies culture. A modern rearing technic has been set up for oyster farming, but for time being, farmers have shown little interest for this species. Results of research concerning short neck clam (Tapes decussatus, T.semidecussatus) have echoed an immediate response from farmers, who are getting organised for this. This new activity shall drive to the construction of hatcheries.

Bivalve shellfish farming in Italy is suffering from water pollution, and the government has consequently introduced a whole set of rules to protect the consumers health. I found this unsatisfactory as it implicitly allows pollution, and solves the problem by excluding farms from the most contaminated areas and by imposing depuration of bivalves by means of costly processes. Sea farmersand fisher men should organise themselves to request that water be cleaned from pollution by industries, cities and agriculture.

SECOND PART : EXPERT REPORTS
SECONDE PARTIE : RAPPORTS DES EXPERTS

PATHOLOGY
–
PATHOLOGIE

SUMMARY OF PATHOLOGY SESSION

L. LEIBOVITZ *

The history of the major epizootic shellfish diseases, their economic impact upon the shellfish industries and the evolutionary development of the regulatory responses to limit mass mortalities in Canada, United States, Japan and France were reviewed by Dr. Henri Grizel. Detailed observations related to the initial appearance, spread, distribution and environmental factors of specific epizootic shellfich diseases in France were presented. From this information, strategies for containment and possible eradication have been developed, but the methods to be used in any particular situation depend on the characteristics of the shellfish operation involved and careful consideration of the economic consequences of the different possible actions.

As a result, limited passive measures have been taken to restrict movements and to market infected shellfish, rather than the more severe, active disease eradication programs.

In attempts to maintain the shellfish industry's economic viability, new resistant shellfish species have been introduced into France and cultured to replace the serious losses from mass mortalities of the cultured native species. In response to the continuing serious disease problems, French governmental agencies, scientists and industry recognized the need for immediate short term as well as long term goals to contain, control, and possibly eradicate these epizootic diseases.

Short term approaches included developing rapid methods for disease identification (diagnosis) to determine the areas where a particular disease is present and to detect movement of the disease within the country. It has been recognized that marketing stocks and reducing biomass were immediate measures of containment for limiting the level of infection.

Long term goals were both basic and applied research to provide a rational basis for prevention, control and eradication. These included identifying etiologies, pathogenesis, and predisposing factors. In the case of infectious agents, they must be isolated, grown in pure culture, and characterized. For viral diseases, molluscan tissue cultures will have to be developed. The basic physiological and pathological response of shellfish to specific disease agents must be understood, including their immunological response. The possibility of shellfish vaccines should be explored. Mathematical and statistical support is needed for a more comprehensive approach to disease epizootiology. From the above body of knowledge, a sound active swift regulatory response for prevention and control of specific epizootic shellfish diseases should be developed to promote the security and economic well being of the shellfish industries.

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* Dept. of Avian and Aquatic Animal Medicine, **New York** State College of Veterinary Medicine, Cornell University, **Ithaca,** New York, U.S.A.
and
Laboratory for Marine Animal Health, Marine Biological Laboratory, **Woods Hole**, Massachussetts 02543, U.S.A.

Continuing the pathology consideration an universal review of abnormal mass mortalites of adult bivalves during the past century was presented by Prof. Louis Leibowitz. Continous observations, comments and reviews of some of these massive mortalities have produced an understanding of the causes and epizootiology of such mortalities, converting the unknown to the known. This process has been continuing, and our knowledge has been extended beyond the diseases of adult shellfish with the development of new shellfish culture systems. The economic development of the shellfish industry was dependent upon the understanding of all stages of the life cycle shellfish for successful efficient cultural production. Abnormal mass mortalities of shellfish embryos, larvae, and juveniles were an important limiting factor in such newly developed shellfish culture systems.

New specific viral, chlamydial, bacterial, algal, parasitic, toxological, nutritional, physiological and neoplastic diseases of specific stages of the shellfish life cycle were reviewed and the importance of congenital (vertical) and horizontal transmission was discussed. The detection of diseases of cultured shellfish may increase our understanding of diseases of wild stocks and the dynamics of population dependent diseases (intensive rearing).

The needs for basic and applied research and international exchange of information to solve the disease problems of a rapidly growing food producing industry was discussed. These include the development of microbiological methods for immediate identification of diseases (diagnosis), development of methods for prevention, control and eradication of diseases of shellfish, the protection of human health and the development of meaningful health certification of shellfish prior of movement. It was suggested that studies of the immune system are needed to assess the feasibility of vaccination, and the possible use of chemotherapeutic agents for disease control should not be discounted without further research.

A review by Dr. Mori of shellfish immunological research was orally presented in his absence by Dr. Eric Mialhe. In general, mollusc did not have specific hemolymph defense factors but nonspecific defense hemolymph factors such as bactericidins, agglutins and phagocytic enhancing substances have been demonstrated. These substances probably represent general manifestations of a total defense capacity and are part of the normal physiological activity of the mollusc. A wide variety of immunological investigative tests have been utilised to evaluate the defense factor responses of Crassostrea gigas tissue extracts, hemolymph and amoebocytes to heteroantigens. Agglutination, precipitin and phagocytic measurement tests have also been performed employing equine, sheep, and human erythrocytic heteroantigens titrated against a variety of tissue extracts and body fluids of C.gigas to detect possible antibody activity and the results of these tests were reported. Also the influence of divalent ions, saccharides, porcinegastric and bovine sumaxillary mucin, selected bacterial strains and temperature upon these responses have been investigated ; seasonal variation of bactericidal activities of oyster digestive diverticular tissues of C.gigas has been measured during an approximate one year period. No specific antibodies were detected in any of these tests, but seasonal differences were found in the other responses. The possible relationship of the physiological state of health of the oyster to nonspecific disease resistance was discussed. The virulence of pathogens and the genetic make up of the oyster may influence the nonspecific response. An in-vitro oyster tissue culture system would be useful for further studies of oyster immunology.

RESUME DE LA SESSION PATHOLOGIE

L. LEIBOVITZ *

L'histoire des principales epizooties des mollusques d'élevage, incluant leur impact économique et l'évolution des réglements pour limiter les mortalités, est faite par le Dr. Henri Grizel, pour le Canada, les Etats-Unis, le Japon et la France. Des observations détaillées sont fournies sur les epizooties en France, en particulier l'etiologie des maladies, leur progression et leur relation avec des facteurs environnementaux. Ces observations ont permis de proposer des stratégies de prophylaxie, mais les méthodes utilisables dans chaque situation dépendent des caractéristiques locales de la conchyliculture et d'une analyse détaillée des différentes conséquences économiques induites par le choix d'une solution.

Par suite, plutôt que de privilégier des programmes d'éradication, des mesures ont été prises pour limiter les transferts et pour favoriser la commercialisation des coquillages parasités.

Pour maintenir la conchyliculture, des essais d'acclimation de nouvelles espèces ont été tentés en France pour remplacer les espèces indigènes sévèrement atteintes par des mortalités massives. Pour répondre aux sérieux problèmes d'epizooties, l'administration française, les scientifiques et la profession ont ciblé des besoins à court et long terme pour contenir, contrôler et si possible éradiquer ces maladies.

A court terme, le développement de méthodes rapides de diagnostic est nécessaire pour surveiller le cheptel des différentes zones d'élevage et pour détecter la propagation de la maladie. Une des mesures immédiatement préconisées pour enrayer la maladie a été la limitation des foyers infectieux par la commercialisation des animaux et par la réduction de la biomasse cultivée.

Les buts à long terme concernent les besoins nécessaires aux recherches appliquées et de bases pour définir les bases rationnelles indispensables aux programmes de prévention, de contrôle et d'éradication. Ceux-ci incluent l'étiologie, la pathogènie et les facteurs de prédisposition. Les agents infectieux doivent être isolés, cultivés in-vitro et caractérisés. Les cultures de tissus de mollusques doivent être developpées pour l'étude des maladies virales. Les réponses physiologiques et pathologiques des mollusques à des agents pathogènes spécifiques doivent être compris, ainsi que les réponses immunologiques. Les possibilités de mettre au point des vaccins et des chimiothérapies et de sélectionner des souches résistantes de mollusques devraient être explorées. L'epizootiologie marine nécessite un support mathématique et statistique approprié.

En plus de l'acquis scientifique, devrait être developpée une législation permettant des interventions rapides pour prévenir et contrôler les epizooties afin de réduire les aléas et de mieux stabiliser l'économie conchylicole.

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* Dept. of Avian and Aquatic Animal Medicine, **New York** State College of Veterinary Medicine, Cornell University, **Ithaca**, New York, U.S.A.
and
Laboratory for Marine Animal Health, Marine Biological Laboratory, **Woods Hole**, Massachussetts 02543, U.S.A.

Le professeur L. Leibovitz complète les considérations pathologiques par une revue des mortalités massives anormales de bivalves adultes observées durant le dernier siècle. La compréhension des causes et de l'epizootiologie de ces mortalités a été induite par des observations continues, des commentaires et des critiques de quelques unes d'entres elles. La continuité de ce processus a permis l'élargissement de nos connaissances au-delà des maladies des adultes, avec le developpement de nouveaux systèmes de culture. La croissance de la conchyliculture dépend de la bonne compréhension de tous les stades de développement de la vie des mollusques. En effet, les mortalités massives anormales d'embryons, de larves et de juvéniles sont d'importants facteurs limitants pour certains nouveaux systèmes de culture.

Une revue est donnée des nouvelles maladies spécifiques des stades de développement des bivalves. Elles sont d'origine virale, chlamydienne, bactérienne, algale, parasitaire ou résultent de pathologie d'intoxication, nutritionnelle et physiologique. L'importance du mode de transmission, horizontal ou congénital, vertical, est discuté. La mise en évidence de maladies sur le cheptel en élevage est de nature à accroître nos connaissances sur les maladies des stocks sauvages et sur la dynamique des populations malades (élevage intensif). Sont également abordés les besoins internationaux pour la recherche et pour l'information afin de résoudre les problèmes de pathologie affectant les productions de nourriture (ex : algues). Ils incluent le développement de méthodes de microbiologie pour le diagnostic, de prévention, de contrôle et d'éradication. La protection de la santé humaine et l'établissement d'un certificat sanitaire significatif, préalable aux échanges, sont également soulignés. Des études sur le système immunitaire semblent nécessaires pour établir la faisabilité de la vaccination. L'utilisation de chimiothérapies pour contrôler les maladies ne semble pas envisageable sans des recherches supplémentaires.

Une revue des recherches en immunologie chez les mollusques, rédigée par le Dr. Mori, a été présentée en son absence par le Dr.E.Mialhe. En général les mollusques n'ont pas de facteurs spécifiques de défense dans l'hémolymphe, par contre des facteurs non spécifiques telles les bactéricidines, les agglutinines et un pouvoir phagocytaire ont été mis en évidence. Ces substances représentent probablement les manifestations générales de la capacite totale de défense et font partie de l'activité physiologique normale des mollusques. Chez C.gigas la réponse de ces facteurs de défense à des hetéroantigenes a été évaluée à l'aide de nombreux tests immunologiques appliqués à différents extraits tissulaires, à l'hémolymphe et aux amoebocytes. Des tests de mesure d'activités agglutinantes, bactéricides et phagocytaries ont été pratiqués avec comme héteroantigène des érythrocytes de cheval, de mouton et humain et des bactéries. L'influence de certains paramètres, tel que le pH, la présence d'ions bivalents ou de saccharides, sur la réponse de ces facteurs de défense a été aussi étudiée ainsi que l'effet "immunisant" d'injection d'heteroantigènes. Des variations saisonnières d'activités bactéricides dans les tissus du diverticule digestif de l'huître C.gigas ont été détectées sur un cycle d'environ un an. Aucun anticorps spécifique n'a été détecté dans un de ces tests, mais des variations saisonnières ont été trouvées pour d'autres réponses. La possibilité d'une relation entre état général de l'huître et sa résistance aux maladies est discutée. La virulence des pathogènes et les caractères génétiques de l'huître influenceraient cette réponse non spécifique. Un système de culture de tissus in-vitro serait utile pour des études ultérieures sur l'immunologie de l'huître.

EPIZOOTIOLOGY OF BIVALVE MOLLUSCS - PROPHYLACTIC MEASURES

H. GRIZEL *

RESUME. L'intensification des cultures a généralement été accompagnée d'épizooties qui s'avèrent être l'aléa majeur en conchyliculture. Les recherches entreprises doivent ainsi concourir à la définition de mesures prophylactiques appropriées aux élevages marins et susceptibles de réduire l'impact de ces aléas. L'analyse des connaissances acquises sur l'étiologie et sur l'épizootiologie des mollusques permet de noter le besoin de recherches analytiques et la nécessité d'accroître les mesures de protection préventive. La prise en compte des résultats épizootiologiques dans les concepts d'amélioration zootechnique et de gestion des bassins est susceptible de limiter les maladies. Enfin, la résolution des problèmes techniques spécifiques à la pathologie des Invertébrés marins est primordiale pour la progression des recherches.

ABSTRACT. Husbandry intensification has generally been followed by epizootics which are the major risk in shellfish industries. The aim of research is thus to define appropriate prophylactic measures in marine husbandry in order to reduce the impact of diseases. Analysing present knowledge of the etiology and epizootiology of molluscs illustrates the need for analytical research and the necessity of increasing zoosanitary prophylaxis. The inclusion of epizootiology results in zootechnical concepts and in shellfish basin management should contribute to limiting disease. The solving of technical problems specific to marine invertebrate pathology is essential to progress in research.

mots-clés: conchyliculture, épizooties, prophylaxies

key words: shellfish industry, epizootic disease, prophylaxis

INTRODUCTION

The shellfish industry is the result of evolution of a gathering activity into a sedentary cultivation activity. This evolution took place by stages, chief among which are the management of natural beds and the conditioning of juvenile and adult shellfish. These various stages may be observed even today in many countries. This evolution generally came about through increased profits, which led operators to increase the number of animals raised on a given space. The result of this passage from an extensive type of operation to an intensive type has been the appearance over time of problems that were hitherto unknown in operations of the early type. Chief among these were declines in growth and quality, variations in fertility rates and the arrival of epizootic diseases. Efforts to solve such problems necessitated the development of specific research that would supplement and complement the empiric knowledge acquired up to that time. These links, which have already been made in the case of land-based husbandry with the introduction at the operator

* Laboratoire de Pathologie IFREMER (IFREMER Pathology Laboratory)
56470 **La Trinité sur Mer**, France

level of genetics, prophylaxis and application of advanced husbandry techniques, must now be envisaged for marine husbandry, which is at a vital crossroads in its development. Among the research directions to be developed, the results obtained in pathology and on the development of appropriate prophylactic measures for marine operations will be determining factors in future successful development.

1. ECONOMIC IMPORTANCE OF EPIZOOTIC DISEASE

The few examples shown in Table 1 indicate, in the first place, that disease causes very large declines in production. The resulting mortality may be massive and sudden, if caused by an acute infestation, or chronic and crippling for operators in the case of high-risk endemic diseases. It may also be seen that all the principal species of oysters have been victims of disease or mortality, and all the major mollusc-producing countries have had to deal with such pathological problems. Study of these diseases has necessitated, and still does, the acquiring of further knowledge of pathogens and their epizootiology, but also of host species and their environment.

2. DEVELOPMENT OF KNOWLEDGE OF MOLLUSC EPIZOOTIOLOGY

Epizootiology may be broken down into several branches, among which are descriptive, analytical and predictional epizootiology.

Since the complexity of studies may vary with the nature of pathogens, we shall briefly recall the etiology of the principal mollusc diseases described to date. The most significant epizootic diseases have been caused by viruses, bacteria, fungi and protozoa. Metazoa belonging to the Crustacean group have also been recognized as mollusc pathogens. As well, a number of rickettsia have recently been described, some of which were co-present with mortality in burrowing bivalves (Kinne, 1983).

2.1 Descriptive epizootiology

2.1.1 Diagnostic techniques

Discovery of a pathogen, whatever the reason may be, and follow-up of its evolution necessitate mastering techniques of ad hoc diagnosis. The most frequently used technique for molluscs is classic histology. In spite of its awkwardness and the risks it implies, it remains the most dependable method for diagnosing a wide range of pathogens. In cases where wide-range health status monitoring is required, it is hard to see what could replace it. For certain specific cases, however, it may advantageously be replaced by the smear technique, which is much quicker and less costly, or else be supplemented by specific techniques if doubt still persists. Examples of this are the culture of *Perkinsus marinus* on a thioglycolate medium (Ray, 1952), or that of *Ostracoblabe implexa* developed by Alderman and Jones (1971).

2.1.2 Space-time evolution

Diagnoses may be performed either at the request of an administration or a professional who wishes to know the health status of his stock, or else in the more general framework of an epizootiological survey. The information collected deals with the occupation rate of the diseases as given by the percentage of parasite-infested batches and with the parasitism rate or

prevalence, which corresponds to the percentage of parasite-infested shells in each batch. Estimating the degree of infection of a subject is often more subjective and would require use of titration methods.

Many studies have been carried out to follow the space-time evolution of epizootic diseases due to *Perkinsus marinus*, *Minchinia costalis* and *M. nelsoni* in the U.S. and to *M. refringens* and *B. ostreae* in France. On a practical level, the results of these epizootiological surveys, although not spectacular, contribute to decisions regarding prophylaxis and inform operators about the operating plans they must follow. Regular analysis of the parisitism rate of *M. Refringens*, for example, made it possible in 1979 to propose a modest resumption of the culture of *O. edulis* in the Morlaix and Penzé centres, in the Crach and St. Philibert rivers and in the Roscanvel sector in Brest harbour.

2.2 Analytical epizootiology

2.2.1 Reproduction of disease

Discovery of a microorganism or a parasite necessitates experimental reproduction of the disease to determine its etiology. Although this can normally be obtained in the ambient environment, it can only rarely be reproduced under laboratory conditions.

A - Experimental contamination in the field

This type of contamination is performed quite simply by introducing shellfish from areas thought not to contain the parasite into sectors where the disease exists. Fairly large control batches are examined prior to each transfer. The introduction process may be relatively simple, depending on whether the stage(s) of infection have been identified or not. The molluscs used are placed in bags or crates in order to prevent any mixing with surrounding populations.

In this way, Andrews et al. (1962) obtained infections of *Minchinia costalis* in *Crassostrea virginica*, and the same was true for the tests conducted by Couch and Rosenfield in 1968 with *Minchinia nelsoni* and *M. costalis*. A more complex procedure, based on repeated introductions at various times of the year (September, December, March and June) enabled them to determine the period at which the first stages of these parasites appear and to study the growth cycle. Too long an interval between the various introduction operations, however, makes it impossible to accurately determine the moment when contamination begins and to establish the duration of this period. These considerations led Grizel and Tigé (1979) to develop a more complete process. Since the infectious stage of *Marteilia refringens* was not known, it was important to determine that the host did not contain any unidentified stages before the disease could be diagnosed. The model used in the study was based on monthly introduction of healthy oysters into a contaminated zone, along with a re-transfer of half of the subjects that had spent a month in the contaminated sector back to their original zone. All batches were systematically checked the month after their immersion, and every month following that.

Using this method, the authors demonstrated that:

- the period of contamination occurred only during the summer period, infectious forms were not present in the host very far in advance, maximum incubation period was a month, and the disease may manifest itself in sites

where it is not present. As well, precise information was obtained on the development cycle.

- A direct effect of these observations was the reutilization of concessions located in parasite-infested sectors for short-cycle culture other than during the summer.

- An experimental model of the same type, but simplified, was also used by Tigé and Grizel (1984) for *Bonamia ostreae*. As opposed to those previously mentioned, this protozoan is infectious all year long. Symptoms of the disease may be detected three or four months after introduction of the oysters. Significant mortality normally occurs three months after the first contamination and may go as high as 90% in 10 to 12 months of rearing.

B - Experimental contamination in the laboratory

Laboratory reproduction of the disease is essential in order to obtain experimental models required for specific, more basic research. It must also allow for the study of mechanisms governing defense in the host and for preservation of parasite stocks.

To date, among all the major recent epizootic diseases, reproduction has only been possible for two species, *P. marinus* and *B. ostreae*. Classic methods of experimental contamination, as described by Ray (1954) are based either on contact within an enclosed space between contaminated and uncontaminated hosts (proximity technique), or through introduction of parasites in suspension with phytoplankton (feeding). Injections through an orifice drilled in the right valve or in the part of the shell between the two valves are also common and have been used by many authors (Balouet et al., 1979; Poder et al., 1982; Bachère et al., 1984). Application of these various procedures enabled positive results to be obtained with *B. ostreae*.

2.2.2 Receptivity of the host

For parasites of *O. edulis*, *M. refringens* and *B. ostreae*, a number of experiments have been carried out on host receptivity. In the case of each different agent, receptivity varied with the genus, species, race and age of the host.

Early stages of *M. refringens* were reported by Cahour (1979) in the stomach epithelium of *C. gigas*, while Tigé and Rabouin (1976) described stages of this parasite in *Mytilus edulis*. Recent research using an electron microscope or serology techniques have conferred on *M. edulis* the status of a species. During acclimatization tests on *Ostrea chilensis*, Grizel et al. (1983) observed that this species was vulnerable to two parasites of *O. edulis*, which caused the same type of lesions, in particular branchial lesions in the case of infection by *B. ostreae*. As well, results of tests carried out on flat oysters *O. edulis* of various origins showed that, whatever their origin, they are vulnerable to *M. refringens* (Table 2). Contamination also took place during the summer period, and the development cycle is comparable for all batches (Grizel, 1979). The same was observed with *B. ostreae*, although significant differences were mentioned by Bachère (1984) between flat oysters of Mediterranean and Atlantic origin.

Age-specific differences in contamination rates were recorded for *O. edulis*: for the two pathogens mentioned above, the percentage of parasite-

infested spat was always very low, in the order of 1%, while in the same sector older oysters showed high contamination rates. Similar observations were reported for summer die-off of *C. gigas*, where the birth cohorts most commonly affected were those of either 12 months or 24 months of age. The same was true in the case of *Perkinsus marinus*, where juveniles were less receptive to the disease.

Ray (1954) states that, statistically, the risk of contamination is likely to be less for juveniles, since their filtration rate is slower than that of adults.

Another observation involves *C. gigas* and *M. edulis*. These two species, found on most continents, have so far experienced few serious parasite infections, in spite of the fact that they are found in zones having a high risk of contamination. Beds of *C. gigas* located near batches of *O. edulis* infested with microcellular parasites, were found to be free of this pathogen (Glude, 1975). As well, Comps (1972) reports the resistance of this oyster to the virus responsible for die-off of *C. angulata* (Comps and Duthoit, 1976). In some cases, *C. gigas* and *M. edulis* may be found to be infected with pathogens of other species without showing any signs of morbidity. They may then serve as carriers.

2.2.3 Influence of physical and chemical parameters

The life of molluscs is highly dependent on variations in the physical and chemical parameters of the ambient environment. Salinity, temperature, oxygen and pollutants are all important and limiting factors that may directly cause mortality or lead to malformations. Within the very broad limits tolerated by molluscs, abrupt variations in these parameters bring on stresses which decrease the resistance of the host or favour the manifestation of microbial pressure. These factors may incidentally also prove to be limiting for pathogens.

Among the physical and chemical parameters studied, salinity is a limiting factor for the development of *Minchinia nelsoni*. Haskin and Ford (1982) demonstrated the relation between development of the parasite, percentage of infection, mortality rates and salinity gradient. The disease regresses with a decline in salinity, with development of *M. nelsoni* being inhibited below 15% (Andrews, 1983). These field observations confirm laboratory experiments by Sprague et al. (1969) on the same species. Conversely, high salinity favoured development of the parasite, and periods of drought were accompanied by fresh attacks of the disease (Andrews, 1968). According to Ray (1954) and Mackin (1956), *Perkinsus marinus* is inhibited or even destroyed at less than 11% salinity. These observations are nevertheless modified somewhat by those of Andrews and Hewatt (1957), who noted no variations in infestation rates following transfer of oysters into a desalinated water, and especially by those of Otto and Krantz (1977), who reported the presence in Chesapeake Bay of a strain of *Perkinsus* that was adapted to low salinity. On the other hand, high salinity may be a factor limiting the propagation of *M. refringens*. It has spread downstream in rivers and its presence has rarely been observed in truly oceanic waters where salinity variations are slight. Observations by Comps (1979) on transfers in Brittany of parasite-infested flat oysters in the Thau pond showed that the cycle of *M. refringens* is normal in the first year after transfer, and then the infection declines and even disappears.

Start-up of the cycle in the spring is disrupted. While many factors may be held responsible, such as culture techniques, physical and chemical components, etc., salinity is the most remarkable of the latter. At this location, salinity is always higher than in Brittany, at 35 to 37%.

Temperature also plays an important role. Experiments by Grizel and Tigé (1979) on *M. refringens* show close correlation between the period of infection by this parasite and temperature. The first instances of contamination take place only during the summer, with the temperature threshold being located around 17°C. The development cycle is also linked to changes in temperature, with a decrease in infestation rates and sporulation occuring during the winter when temperatures drop. These relations were also shown by Farley (1975) for *Minchinia nelsoni*, whose growth cycle is quite similar to that of *M. refringens*. Low temperatures may, however, favour the presence of *Hexamita inflata*. Scheltema (1962) reported winter die-off in Delaware Bay linked to *Hexamita*. The noteworthy characteristic of this parasite is to be present and cause mortality whenever shellfish undergo stress. This saprophyte becomes a pathogen in oysters subjected to temperatures around 0°C or lower, or stored in poor conditions or in environments with low oxygen saturation rates (Shuster and Hillman, 1963).

2.2.4 Influence of cultural parameters

Cultural parameters may influence the onset of a disease as well as its spread.

One of the most important of these is probably rearing density which, by influencing growth and the health status of the host, may diminish its sensitivity and facilitate spread of the parasite, since the chances of the host coming into contact with the pathogen are much greater. In 1952, Korringa had observed that densities of *Mytilicola intestinalis* increased with those of the host population. In this case, the increase brought on pathogenic effects and even mortality, in particular when the number of parasites is greater than 10 per mussel. Fenchel (1966) claimed that the number of parasite species may also increase with host densities. This author reported the presence of 6 or 7 species of ciliata in dense populations of *Mytilus edulis* and *Macoma balthica*, whereas they normally contain only one or very few.

The culture technique used may also have consequences on mortality rates. Koganesawa (1975) reports the appearance of massive mortality in Hiroshima Bay in Japan coincident with the development of suspended culture, which led to an increase in productivity. In France, notable differences have been observed between the development of diseases in oysters reared in deep water and those cultivated in the intertidal zone.

These differences essentially depend on environmental conditions, since the water masses changed are large, parasite dilution is greater, trophic inflow is normally satisfactory and turbidity does not hinder filtration functions. Thus *M. refringens* has never spread in the open bays of Brittany (Quiberon, St. Brieuc, Cancale), in spite of large transfers of parasite-infested oysters. Hepper (1955) mentions similar observations for *M. intestinalis*. In Holland, rearing of mussels in deep water at lower densities has been suggested by Korringa (1957) to limit the action of this parasite. The practice of transferring animals from one centre to another normally presents cultural advantages, since the qualities of some beds

are superior to others for growth or obtaining quality shellfish. During critical periods, however, these methods are to be condemned, since they permit and favour the spread of pathogens. We are reminded here of the case of *B. ostreae*, whose introduction into Denmark, Holland, Spain and even perhaps England did not occur by accident. The same is true of its spread in Brittany.

3. PREDICTIONAL EPIZOOTIOLOGY - PROPHYLAXIS

According to Ravaud (1984), pathology among animals is the end result of destruction of the balance between the resistance potential of subjects and the pathogenic force of many aggressive factors, some of which may be determining in themselves.

Negative changes in the key factors regarding culture, such as biomass and transfers, are consequently likely to increase the risks of an epizootic disease developing. An increase in biomass is in fact a parameter that works in favour of the spread of disease, but in addition, in the case of filter-feeders, it is a parameter that may work against growth and mollusc quality. Transfers between basins and between countries may encourage the introduction of foreign diseases or the spread of an indigenous disease. The implementation of intensive rearing thus necessitates a very specific sort of analysis, since the profits expected from this type of rearing should not, on the average, be less than the effects resulting from the attendant disadvantages.

In such cases, working out prophylactic strategies takes on great importance and can only be based on knowledge gained regarding the host, the pathogens, the environment and the zootechnical and technical conditions of the operation. To date, however, contrary to developments observed for land husbandry, no country has truly developed a structured policy of marine prophylaxis nor defined actual strategies. Research has mainly been carried out once a disease was discovered, and in most cases any action taken was on a case by case basis. Varying results were thus obtained for the various main types of prophylaxis.

3.1 Veterinary prophylaxis

The purpose of veterinary prophylaxis is to reduce to the lowest level possible the risks of introducing and spreading parasites. Prevention programs have been developed in various countries. Apart from legislative measures and monitoring, methods basically involve diagnosis and setting up inspection systems. These measures apply to both imported and indigenous stocks.

3.1.1 Imported stock

All countries have passed laws aimed at regulating imports, the basic principle of which is the prohibition of immersion. In certain cases, defined by procedures specific to each country, exemptions may be allowed, in particular for juveniles.

3.1.2 Indigenous stock

Measures taken once a disease is declared basically deal with transferring and possibly destroying stock. Disinfection of equipment may also be required,

as was the case in Holland when vessels were transferred from Yerseke Bank to Grevelingen. The results of these different measures vary. The effectiveness of prohibiting transfers is linked to the quality of the inspection system for early diagnosis of disease, to the efficiency of the administration in passing laws and regulations, and to the willingness and potential to apply them. The impact of mass destruction on development of the disease is so far difficult to quantify. Some positive results appear to have been obtained, particularly in deep waters, but these experiments are as yet too recent to be conclusive. In any case, they do not appear to have had any noteworthy positive effect on intertidal beds, where diseases such as marteiliosis and bonamiosis are still active. The degree of virulence of pathogens, the presence or absence of a heteroxenous cycle and the presence of intermediate hosts are all factors that may limit the effectiness of mass destruction.

3.2 Zootechnical prophylaxis

The purpose of zootechnical prophylaxis is to improve rearing techniques and concepts to obtain animals in better condition and to find more resistant animals.

3.2.1 Improving rearing conditions

Improving rearing conditions normally leads to gains in growth and quality and an increase in survival rates. We have seen that certain cultural parameters may engender mortality or facilitate the spread of pathogens.

Parameters on which action may be taken to improve production are such things as reduction of stress, choice of planting dates, quality of food provided, particularly for artificially reared stock (hatcheries and nurseries), site characteristics, transfer dates and numbers, reducing rough mechanical handling in facilities, improving basin storage conditions and reducing storage times, and controlling the biomass under culture.

Considerable progress has already been made with the development of suspended, ground-level and deep-water culture, in the areas of improving beds, developing more efficient machinery and equipment, in particular for mussel-rearing, and also in techniques of producing juveniles of several mollusc species. Many more zootechnical improvements may be be developed, although these will not necessarily result from spectacular technical changes.

3.2.2 Genetic improvement

At the present time, very little is being done in the field of genetic improvement aimed at increasing the resistance of a species to one or more diseases, and work underway deals with optimizing natural resistance characteristics. Work was carried out in this direction by Drinnan (1967) in Canada in the case of Malpeque disease. Gradually building up a stock of oysters that had survived the disease enabled him to obtain descendents whose survival rate was higher than that of control oysters which had never before been in contact with the pathogen. This procedure was reutilized by Haskin and Ford (1979) to creat strains of *C. virginica* that were more resistant to *Minchinia nelsoni*, but the results of this work are still in the very early stages. The same principle was successfully used by Beattie et al. (1980) to select stocks of *C. gigas* that would be less susceptible to summer die-off.

3.2.3 Replacement of one species by another

Replacement of one species by another must be considered exceptional, given the disadvantages presented by such operations, in particular increased risk of introducing pathogens and new species. In extreme cases, however, it may appear desirable, for the good of the industry as a whole, to attempt to acclimatize species whose biological characteristics are close to those of indigenous species. This was attempted, without success, with *O. chilensis* in England and France. This species, apart from a marked sensitivity to low and high temperatures, proved to be receptive to *M. refringens* and *B. ostreae* (Grizel et al., 1984). Conversely, *C. gigas* was successfully introduced in a number of countries, notably in France, where it proved to be resistant to the iridovirosis affecting *C. angulata*.

3.2.4 Diversification of culture

Diversifying cultures may also prove to be a wise prophylactic method. A judicious choice of species for rearing may reduce inter-specific trophic competition and make for better use of coastal space. As well, the specific nature of parasites, observed for the majority of mollusc pathogens, seems to indicate that a better quantitative distribution of species in a given geographic area could aid in reducing microbe pressure. The practice of polyculture should also make shellfish-rearing enterprises more feasible, even though they still remain exposed to a number of risks. There is obviously only a limited choice of species (various clams and scallops, cockles, etc.), but zootechnical progress over the past five years may lead to interesting development possibilities in the not too distant future. Multispecies operations already exist in the United States and are beginning to appear in Europe, both at the level of the individual operation and for entire shellfish basins.

3.3 Medical prophylaxis

In the present state of knowledge, it is hard to conceive of medical forms of prophylaxis. Individual treatment is out of the question, for cost reasons; similarly, it is hard to imagine the repeated use of therapeutic agents. Laboratory research being carried on in this area has so far not yielded any practical applications, either because the treatments studied are not effective (Grizel, 1979), or are too difficult to apply (Ray, 1966). It is nevertheless possible to conceive even now of treatment in closed or semi-closed environments. This would basically deal with larval pathology caused by bacterial contamination, which might be prevented or reduced by the use of broad-spectrum antibiotics.

4. DISCUSSION - CONCLUSIONS

Applied research work on disease and disease-causing agents is inconceivable without the prospect of eventually arriving at proposals in the area of prophylaxis. To achieve this, three types of complementary action are required:

- prevention, by implementing regular health-status inspection of stocks,
- improvement through development of more rational culturing methods and techniques, but also through zootechnology and genetics,

- curing disease, through investment in research in as yet unexplored areas of marine pathology.

Progress in these various avenues will be impossible, however, without first defining a structured long-term research policy and without overcoming the technical problems that currently limit investigations to descriptive research, to the detriment of analytical research. There are number of strategies and broad research areas that might be examined to promote positive development of research on the pathology of marine bivalve molluscs.

With respect to zoosanitary prophylaxis, experience to date has shown that, while it is relatively simple to detect and describe parasites, it is much more difficult to determine at what point these actually become pathogens for the host. Diagnosis of this critical period, during which the parasite passes from a state of equilibrium with the host to a state of imbalance, is extremely important. It should correspond to the implementation of specific measures, in particular prohibition of transfers, which would suffice to limit the spread of the disease. Response and reaction time should thus be as short as possible if measures are to be effective. To this end, it may prove useful to set up a permanent inspection system, whose effectiveness would depend on the analysis capacity and the quality of diagnosis. Efforts to design sampling plans and develop diagnostic techniques can only improve the results already achieved. This research might be complemented by the creation of information files centralizing data on techniques used, oyster history, general environmental conditions and the state of stocks. These methods, developed by Tillon et al. (1980) and by Madec and Josse (1981) for land husbandry, might serve to bring to light factors that may play a role in the introduction and spread of disease, but also to better pinpoint critical periods in the course of a disease.

Developing zootechnical prophylaxis will require the formation of interdisciplinary teams working toward a common goal. Since the main criteria are improving stocks and their resistance, it would appear desirable to arrive at a definition of the typical biological, physiological and biochemical characteristics of a healthy mollusc.

Progress in the medical prevention of disease is linked to learning more about pathogens and their hosts. The main technical obstacles at the present time are related to purifying parasite strains and the development of cell cultures. Solving the first problem would open up prospects for research into the development of serological diagnosis, disease reproduction, the biochemical composition of parasites and molecules that might eliminate these parasites. Removing the second obstacle is a necessary preliminary to the study of microorganisms, but also to the understanding of the cell systems of the host. In addition, the development of reproducible experimental models, notably for the study of disease transmission and the preservation of parasite stocks, will lead to progress in research, especially into mollusc defence mechanisms.

In conclusion, marine farming, in particular shellfish-rearing operations, is in a critical phase, as the result of increased human pressure (industrial, tourist, urban, cultivation) and biological pressure (epidemics). Empirical concepts must consequently be supplemented by organized research which will enable solutions to be found for certain problems, but which will also provide useful elements for decisions on future developments. Among

these, definition of prophylactic strategies appears to be particularly important, given the impact of epizootic disease on the shellfish industry. These strategic decisions will necessitate the forming of interdisciplinary teams, but also closer relations between the various government bodies involved and the industry. Members of this industry do not yet have a full understanding of changes currently taking place, and it is vital that they should be kept informed so that they can grasp the rationale of all these measures.

COUNTRY	CANADA	U.S.A.	JAPAN	FRANCE	
Disease	Malpeque disease	Minchinia nelsoni	Summer die-off Matsushima Bay	Iridovirosis	M. refringens B. ostreae
Host	C. virginica	C. virginica	C. gigas	C. angulata	O. edulis
Years	1934-1940	1954-1975	1961-1964	1970-1971	1969-1985
Impact on production	9000 barrels down to only a few	3.5 10^6 bushels to 095 bushels	50% mortality per year (stocks of 1500 T)	60 000 tonnes down to nil	15 000 tonnes to 1000 tonnes

Table 1: Impact on production of the principal oyster diseases

ORIGIN \ MONTH	March	April	May	August	Sept.	Oct.	Nov.	Dec.
Flat spat Morbihan control				1/17	15/20	22/25	17/19	20/22
Flat spat Mediterranean				1/22	18/20	18/22	18/19	19/23
Spat Hatchery					14/23	10/17	15/20	6/20
Hatchery spat "Pied de Cheval" variety					3/4	16/9	6/12	5/20
Adults 0/20 Ireland				4/13	5/12	17/20	17/20	12/20
Adults - Mediterranean Greece		0/30			18/19	11/11		

Table 2: Contamination test on flat oysters of various origins and ages (Crac'h river, 1976) using *M. refringens*

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ABNORMAL MORTALITIES APPARENTLY UNRELATED TO KNOWN PATHOGENIC AGENTS

L. LEIBOVITZ *

3STRACT : A review of reported mass mortalities of adult bivalve molluscs during the past century was presented. Continuous observations, comments and reviews of some of these massive mortalities have produced an understanding of the causes and epizootiology of such mortalities, converting the unknown to the known. With the development of new shellfish culture systems, our knowledge has extended beyond the diseases of adult bivalves. The economic development of the shellfish industry was dependent upon the understanding of all stages of the life cycle for successful efficient production. Mass mortalities of shellfish embryos, larvae, and juveniles were an important limiting factor in such newly developed shellfish culture systems. New specific viral, chlamydial, bacterial, algal, parasitic, toxicological, nutritional, physiological and neoplastic diseases of specific stages were reviewed. The importance of congenital (vertical) and horizontal transmission was discussed.

The detection of diseases of cultured shellfish may increase our understanding of diseases of wild stocks and the dynamics of population density dependent diseases (intensive rearing). The need for the development of microbiological methods for immediate identification of disease (diagnosis), methods of prevention, control and eradication of diseases of shellfish, the protection of human health and meaningful health certification of shellfish prior to movement were indicated. A research program with the above objectives was required to achieve the technological development of a economically sound commercial shellfish industry, both nationally and internationally.

RESUME : Les mortalités massives observées au cours du siècle dernier sont passées en revue. Le suivi de quelques unes de ces mortalités massives et les analyses et synthèses qui en ont été faites, ont permis de comprendre les causes et l'épizootiologie de telles mortalités, et de passer du domaine de l'inconnu à celui du connu. Le développement de nouvelles méthodes conchylicoles a permis l'extension de nos connaissances au-delà de la pathologie des adultes. Le développement de la conchyliculture dépendait de la connaissance de tous les stades du cycle pour réussir une production efficace. Les mortalités massives des embryons de mollusques, des stades larvaires et juvéniles, étaient un facteur limitant important, pour les systèmes d'élevage développés récemment. A chaque stade sont présentées les nouvelles maladies virales, chlamydiales, bactériennes, algales, parasitaires, toxicologiques, nutritionnelles, physiologiques et néoplastiques.

* Dept. of Avian and Aquatic Animal Medicine, **New York** State College of Veterinary Medicine, Cornell University, **Ithaca**, New York, U.S.A.
and
Laboratory for Marine Animal Health, Marine Biological Laboratory, **Woods Hole**, Massachussetts 02543, U.S.A.

L'importance des transmissions congénitales (verticale) et horizontale, est discutée. La détection des maladies des mollusques en élevage permettrait d'améliorer notre compréhension des maladies des stocks naturels et des maladies liées à la densité (élevage intensif). Sont indiqués le besoin pour le développement de méthodes microbiologiques permettant une identification rapide de la maladie (diagnose), préventives, de contrôle et d'éradication des maladies des mollusques, et la nécessité de protéger la santé publique et d'un contrôle sanitaire sérieux des coquillages à la source. Un programme de recherche comportant les objectifs précités est nécessaire au développement technologique de la conchyliculture sur des bases économiques solides, au niveau national et international.

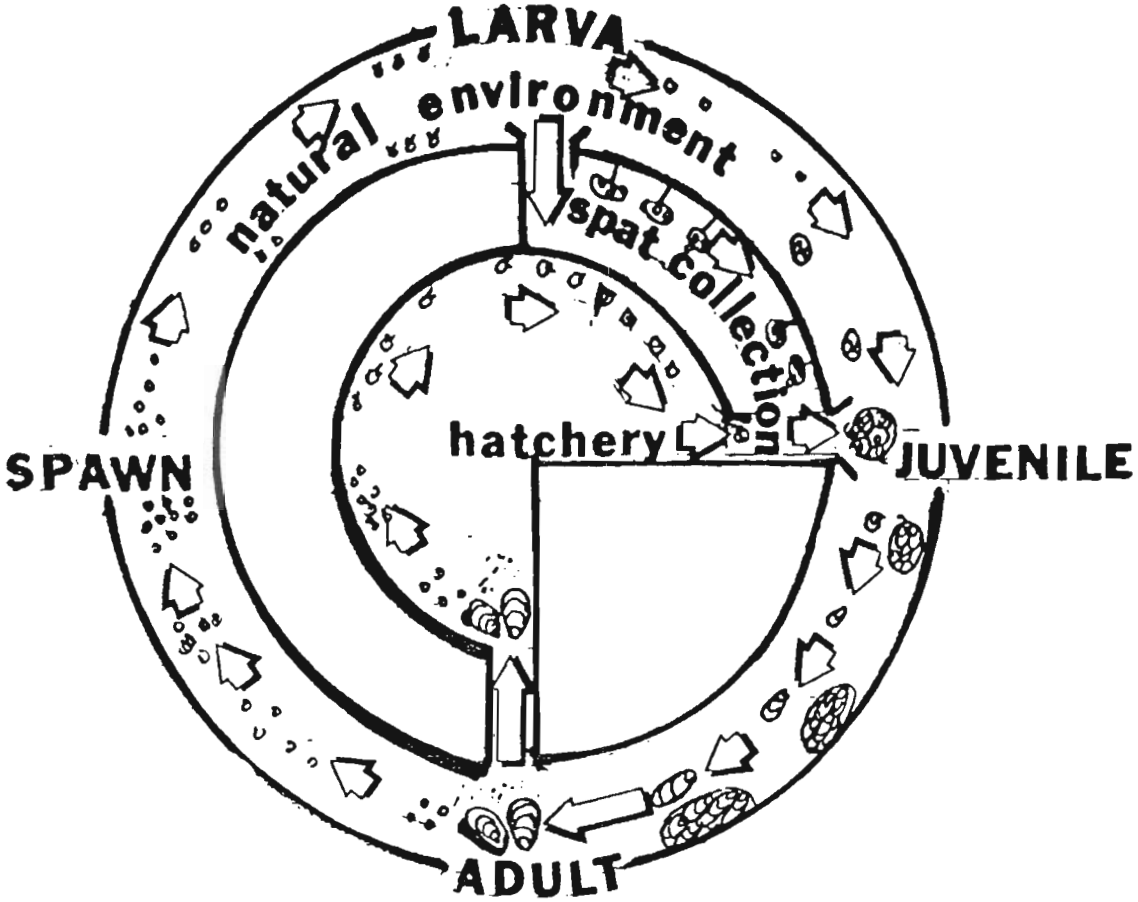

Figure 1. Diagrammatic Comparison of Shellfish Life Cycles in 3 Methods of Culture.

Outer ring represents natural culture.
One-fourth segment of middle ring represents spat collecting culture.
Three-fourths segment of inner circle represents hatchery culture.
All methods employ natural growout of juveniles and adults.

INTRODUCTION

Historically, mass mortalities of adult bivalves have been frequently and universally reported (Sinderman 1968a, 1968b, and 1970). Mortalities of short duration have been poorly documented; however, those of cyclic or long durations have been subjected to more detailed investigations and continuous commentaries during the last century (Montauge 1878; Fabre-Domergue 1887; Giard 1894; Herdman 1896; Orton 1924; Gineste 1925; Roughey 1926; Needler 1931; Dexter 1944; Mackin 1951; Andrews 1956; Logie 1956; Kodera et al. 1958; Haskin 1961; Dickie and Medcof 1963; Kan-no et al. 1965; Mori et al. 1965; Comps 1970; Grizel et al. 1974; Krantz 1982). Attempts were made to define the diseases responsible for the abnormal mortalities and their possible causative agents. This process included naming the disease for the area in which it was found (e.g. Dennan Island disease, Malpeaque Bay disease, etc.) or the anatomic lesions produced (La Maladie des branchies, La Maladie du pied, etc.) or cryptic references to unidentified disease agents found in oyster tissues (Multi-Sphere Unknown (MSX), Microcell disease etc.).

After repeated studies, epizootiological data have been collected in many cases which defined the geographical, seasonal, environmental, species and age predispositions to disease. In some cases, specific lesions and physiological alterations were demonstrated and specific pathogenic agents were identified. Accordingly, this long-term extensive process of repeated observations and commentaries was required to establish the identity of the etiological agent of the disease, its pathogenesis, and the needed epizootiological data. Results of such studies transformed the abnormal massive mortality entity into a known disease.

With the depletion of natural shellfish stocks, artificial culture of shellfish is being rapidly developed. New concerns for disease prevention have appeared following the introduction of such culture systems. The potential introduction, proliferation, and worldwide distribution of exotic diseases, predators, fouling agents and pests becomes a real possibility with the great productive capacity of shellfish hatcheries and our rapid methods of transportation and distribution (Mann 1978).

We are no longer limited to natural populations of adult shellfish and spat collection in natural bodies of waters. We must now be cognizant of diseases of all of the life stages of shellfish in either natural or artificial cultural environments. Since artificial cultivation requires the provision of all of the physiological needs of shellfish at all stages of the life cycle, we are now detecting diseases and massive die-offs related to improper aquatic environments, metabolic imbalances, reproductive diseases, congenital and reproductive disorders, and genetic defects. We are now detecting the so-called "childhood diseases" of larval and juvenile shellfish which produce mass mortalities in cultured replacement stocks. Understanding of these diseases gives us our first insight into diseases of wild larvae and juveniles. In these new-culture systems, we are discovering "unnatural" diseases related to concentrated massive shellfish populations not found in natural environments. The ease of detecting shellfish diseases in culture systems may allow opportunities for study that would not be easily found in natural environments.

Within the above framework, the following considerations of abnormal mass shellfish mortalities will be reported and reviewed.

I. The Relationships of Mass Mortalities to Stage of Development

A. Embryos

While it is known that embryo survival is dependent upon proper environmental temperatures, food availability and compatible water quality, little is known of the fate of wild embryos in natural waters. In addition to predation during the planktonic stages, unfavorable environmental conditions have been cited as causes of mass embryo mortalities in the wild.

In shellfish hatcheries, where ova are collected and fertilized, embryo mortality may range from 0 to 100 percent (Fig. 1). Bacterial diseases are common, and are often associated with improper handling, contamination and excessive concentration. Lipovsky (1984) reported that the percentage development of embryos to straight hinge larvae decreased from 80 to 20% as the hatchery spawning season progressed. Poor embryo development and liveability have been attributed to improper brood stock conditioning. Abnormal embryo development has been attributed to genetic factors, polyspermia, malnutrition, adverse embryonating conditions and intoxications.

B. Larvae

Massive mortalities of cultured shellfish larvae are not uncommon. Mortality rates are usually inversely proportional to larval age or maturity (Walne 1974). The percentage mortality may range from 0 to 100 percent (Fig. 1) for individual larval cultures. Mortalities may occur suddenly in hatcheries that have been relatively free of disease problems. In the Northeastern Atlantic coast region of the United States, such mortalities are more common during late winter and early spring (February and March) and at peak water temperatures during summer months. Newly constructed hatcheries tend to have higher mortality rates than older established hatcheries, suggesting that hatchery management influences mortality rates.

1. Mortalities of cultured larvae associated with bacteria

Bacterial diseases of larval shellfish have been well documented as one of the most important causes of larval mortality (Walne 1956; Guillard 1959; Tubiash et al. 1965; Brown 1973; Prieur 1974; Leibovitz 1978a, Leibovitz 1978b). While specific pathogens such as Vibrio spp. and Pseudomonas spp. have been clearly identified as causes of massive larval mortalities, many species of bacteria are facultative larval pathogens. These bacteria are dependent upon physical and chemical shifts in the aquatic environment that favor bacterial proliferation and invasion of larval tissues. Such shifts are promoted by increased temperatures and eutrophication of the culture system by increased organic loading of the culture vessel with feces, food and foreign material.

Many bacteria, including Vibrio spp., have surface coating properties and are ideally suited for growth on the conchiolin surfaces of shellfish valves and hinges (Elston et al. 1982). Such bacterial populations have been incriminated as causes of shell fragility, growth depression and mortalities in cultured shellfish. In addition, such organisms can be congenitally transmitted by the brood stock to the embryonic stocks at time of spawning.

2. Viral disease of larval shellfish

Although a number of viruses have been found in adult shellfish, only a single viral disease has been described in larval shellfish (Elston 1979). The disease was found in both wild and cultured Pacific oyster larvae and is associated with mass mortalities. Although suspicion of the disease can be based upon light microscopic examination of infected larvae; confirmation requires electron microscopic examination. Although other viral infections

have been described in adult shellfish, the transfer of such viral infections to larval shellfish is unknown at present. Since viruses are best isolated and identified in cell tissue cultures, the lack of molluscan tissue cultures limits examinations for shellfish viruses.

3. Chlamydial disease of larval and juvenile shellfish

A new serious chlamydial infection of the digestive tract of cultured larval and juvenile bay scallops (Argopecten irradians) has been observed in New England (Leibovitz, in preparation). The disease has produced mass mortalities approaching 100 percent. Characteristic histopathological lesions are suggestive of the disease, but electron microscopy is required for demonstrating the chlamydial organisms in the swollen epithelial cells of the digestive tract of larval and juvenile bay scallops. Late stages of the disease are characterized by desquamation of the epithelial cells of the digestive tract and death. Since the course of the disease is rapid (2 to 4 days), mortality is usually the first sign noted by the hatchery operator. The disease has not been observed in wild bay scallops. This chlamydial agent resembles the organism described by Morrison and Shum (1982) observed in captive adult bay scallops. They did not attribute mortality to the observed agent. Studies are needed to determine whether this agent produces a highly fatal disease in young scallops ("childhood disease") and an inapparent disease in adults.

4. Larval and juvenile mortalities associated with algal organisms

a. Mortalities of larvae associated with Chlorella-like algae

A disease of larval Pacific oysters (Crassostrea gigas) is associated with impaction of the stomach with Chlorella-like algal organisms. The stomach became greatly distended with the organisms and the intestines became impacted with fragments of the wall (Leibovitz et al. 1978). The disease occurred in both cultured and wild larvae.

b. Mortalities of larval and juvenile bay scallops (Argopecten irradians) associated with the dinoflagellate, Prorocentrum spp.

A massive die-off of larvae and juvenile cultured bay scallops was associated with a specific bloom of the dinoflagellate, Prorocentrum sp. in the hatchery's estuarine water supply. Affected scallops evidenced gaping, impaction of the pallial cavity with Prorocentrum organisms, traumatic injuries produced by penetration of the soft tissues by the spine-covered dinoflagellate, and high mortality rates. In some cases, the impacted spines dissected and detached the mantle free from its valvular attachments, leaving the soft internal tissues of the larvae and juveniles exposed. Later during the course of the disease, melanization of traumatic lesions occurred with secondary invasion of bacteria and ciliates (Leibovitz et al. 1984).

Gross and histopathological lesions of the adductor muscle of wild adult bay scallops were found to consist of encapsulated fibrous tissue containing Prorocentrum spp. These lesions were not associated with mortality of adult scallops. The extensive organization of this encapsulated lesion around the organism suggested that the lesion was of long standing and was acquired at a younger age.

c. Mortalities of larval and juvenile hard clam (Mercenaria mercenaria) associated with dinoflagellates of the order Pyrocystales

Sudden mass mortalities of juveniles cultured in upflow culture systems were associated with the ingestion of algae belonging to the order Pyrocystales. The algae were small thin-walled spherical cysts which contained cresent-shaped cells that underwent transverse divisions forming gymnodinoid zoospores with a single longitudinal-directed flagellum. In

histologic sections of the juveniles, the algal cysts could be seen moving through the pallial cavity, into the esophagus, stomach, digestive diverticulum and intestines. Swelling and lysis of the epithelial cells that lined the digestive tract could be observed to parallel the passage of the organisms through the respective lumina. The most severe changes were noted in the digestive diverticula. The glandular epithelium increased greatly in size, obliterating the lumina of the organ, which displaced all lateral organs outwardly. The mantle, gills and outer margins of the digestive diverticula became greatly shrunken and compressed against the inner surface of the valves. Fragments of the algal walls, cresentic bodies and gymnodinoid zoospores could be observed within the greatly swollen cells of the digestive diverticula. In more advanced alterations, epithelial degeneration, dissociation, and necrosis were observed. Late stages were devoid of digestive epithelial cells; only the basal supporting membranes and glandular septa could be seen in histological sections (Leibovitz 1985).

d. Mortalities associated with toxic substances discharged in marine waters

The discharge of toxic substances into marine waters has become a serious cause of mass embryonal and larval shellfish mortalities, especially in highly industrialized or populated coastal areas (Davies and Pirie 1978; Bayne et al. 1978). Hatchery experiences (Sigler and Leibovitz 1982) and toxicological studies (Calabrese 1972) have confirmed such lethal effects. A great variety of toxic substances have been found in the marine environment. In fact, shellfish have been suggested for use as monitors of the marine environment (Goldberg 1975). Die-offs caused by such pollution are difficult to diagnose and document as being the cause of such mass mortalities. The need for diagnostic capability for immediate recognition of toxic shellfish environments is great.

In addition to the acute lethal effects upon shellfish populations, long-term effects on growth, liveability, and reproduction are equally serious (Barzcz et al. 1978).

e. Mass larval mortalities associated with gas bubble disease

The supersaturation of hatchery water systems, due to introduction of air under pressure into water supplies, or temperature differentials of water, is a common overlooked cause of cultured larval mortalities.

C. Mass Mortalities of Juvenile Shellfish

1. Mortalities associated with fouling

Cultured juvenile shellfish are much more resistant to disease than embryos or larvae. Following metamorphosis, many species are sedentary and face new disease problems as juveniles. The most universal and greatest losses of juveniles are associated with fouling and predation. With the advent of culture systems, juveniles are concentrated in great numbers in limited volumes of seawater. Eutrophic conditions generally develop with the accumulation of food, excreta and fouling material during the cultural process. These conditions may favor extensive blooms of competitive flora that are harmful for cultured shellfish. Each fouling agent has a specific effect. Some of these fouling agents may produce respiratory embarrassment by occluding the entire external surface of the juvenile (e.g. bacteria, Vorticellidae, Entoprocta, and blue-green algae). Others may produce cracks, fissures, and cavities in the developing valves and hinge (e.g. pennate diatoms, Folliculina spp.). Bacterial invasions and adhesions of visceral organs develop and rupture of the hinge ligament may follow. Since many of

the fouling agents compete for food with the cultured juveniles, inhibition of growth may occur. Blooms of fouling organisms may displace normal juvenile foods, sometimes with serious harmful effects. The stomach, digestive diverticula, and intestines may become impacted with indigestible material and death may follow obstruction of the digestive tract (e.g. pennate diatoms). Retrograde diseases are common in heavily fouled cultured shellfish. These diseases may cause delayed massive die-offs in newly purchased or planted seed shellfish replacements. Such mortalities are often overlooked as the juveniles die unobserved in natural waters. The health of juveniles must be evaluated by histological examination of the internal organs prior to seeding to determine their potential for growth and liveability (Leibovitz 1985).

D. Abnormal Mass Mortalities of Adult Shellfish

Perhaps mortalities of adult shellfish have been studied more extensively than those of any other stage of the life cycle. In spite of the investigational efforts, the etiology of some mortalities has not been defined. The lack of a known specific disease response of given species of shellfish to environments and nutritional variables adds to the complexity of interpreting such mass mortalities. The following is a consideration of some of these variables:

II. Environmental Variables

1. Temperature

Temperature is one of the chief environmental variables in the successful culture of poikilothermic shellfish, with distribution in natural waters of temperatures ranging from 34-97°F (Galtsoff 1964). The external temperature directly affects respiration and oxygen availability, feeding and water transport, metabolic rate and energy expenditure, and theoretically the immune and pathologic response to disease agents. Shellfish reproduction is also temperature-dependent and accelerates nutrient depletion, making the animal more susceptible to disease. Since shellfish are dependent upon adequate water exchanges the loss of ciliary motion at high temperatures may prove lethal, especially when combined with high salinities (Mackin and Ray 1950).

A representative example of abnormal massive mortalities associated with temperature effects has been the case of Pacific oyster (C. gigas) culture in the Northwestern coastal area of the United States (Lipovsky and Chew 1972). In Japan and the United States, these die-offs have also been associated with highly eutrophic conditions (Koganazawa 1975), bacterial infection (Grischowsky and Liston 1974), and nutritional depletion following spawning. It is possible that all of these contribute to the onset of the disease. More work is needed to reproduce the disease experimentally before the specific etiologic agents are defined. One approach has been suggested to develop genetic stocks which can tolerate the above conditions (Hershberger et al. 1984).

2. Salinity

Although shellfish will tolerate a wide range of salinities, specific species have optimal range levels in specific geographical environments. Thus Galstoff (1964) suggested a range of salinity of 5-40 ppt, but Chanley (1957) reported an optimal for Crassostrea virginica between 15-22.5 ppt in the Atlantic Northeast coast of the United States, and Van Sickle et al. (1976) reported optimals of 5-15 ppt for Louisiana coastal waters in the United States. Direct effects of salinity are related to the range and suddenness of

change (Galtsoff 1964). Lowered salinity has been directly related to increased shellfish mortalities (Butler 1949). High temperature combined with high salinity has a much greater adverse effect than either variable alone, and has been associated with mass mortalities (Owen 1955). The positive effect of sudden lowered salinity is the reduction in shellfish predator populations. High salinity and high temperature also favor many infectious agents (e.g. Minchina, Perkinsus).

3. Substrate

Each species of shellfish has optimal physical substrate. Most oysters grow best on bottoms that are firm and stable. They do not grow well on sandy or soft mud bottoms. Shifting sand will be abrasive and cause valve damage, while mud or silt will cause suffocation. It is possible for oysters to overcome such conditions by elevated oyster reef formations or by being elevated by staked culture or rafts artifically.

Sedimentation and turbidity are quantitative factors that may be beneficial if limited, and lethal if excessive. The availability of planktonic foods may be limited if such turbidity inhibits light needed for planktonic food synthesis.

Increased dredging activities, storms, and strong currents can rapidly convert a favorable habitat to a lethal one by smothering shellfish populations.

4. Nutrition

The quantitative intake of water by shellfish can be enormous. The American oyster (C. virginica) can filter 10 to 20 liters of water for each milliliter of oxygen consumed (Jorgensen and Goldberg 1953). Under normal conditions, this would be equivalent to filtering 1,500 liters (396 gallons) of water daily. One can only speculate as to the foods found in this total volume of water, and the day-to-day variability of the food and non-food elements contained in such a volume. While much consideration has been given to the study of foods beneficial to shellfish, very little attention has been given to substances ingested that are harmful to shellfish and displace natural foods, resulting in malnutrition.

5. Oxygen Depletion

Although often suspected, environmental oxygen depletion in the marine environment is seldom documented as a cause of mass shellfish mortalities. One such documentation of a mass mortality of surf calms (Spisula solidissima) and ocean quahogs (Artica islandica) has been made (Murawski 1977). The above mass mortality was attributed to unusual meterological and hydrographic conditions, combined with an extensive and persistent algal bloom, resulting in oxygen depletion. An estimated 147,000 metric tons of surf clams, 6,600 metric tons of ocean quahogs, and lesser amounts of sea scallops were lost (Sindermann 1979). Similar massive mortalities of sea scallops (Plagopecten magellanicus) have been reported but have not been documented as being caused by environmental oxygen depletion (Medcof and Bourne 1964).

6. Population Density

Although poor growth and development have been attributed to excessive population densities in both wild and cultured shellfish, massive mortalities in such populations have been poorly documented. One report by Kodera (1958) indicates massive die-off of the scallop, Hotategai (Patinopecten yessoensis)

in Mutsu Bay, Japan, related to high densities, resulting in pileups, inserting one scallop into another with lethal effects. Similar mass mortalities have been reported in sea scallops (P. magellanicus). It is likely that motile scallops are predisposed to traumatic lethal injuries when overcrowded.

7. Pollution

Pollution has been of serious concern to the shellfish industry. It is likely that it is often overlooked and difficult to diagnose as a cause of mass shellfish mortalities. Obvious visible causes, such as oil-spills, are dramatically in evidence. Such was the case of the oil-spill of the "Amoco-Cadiz" (Michel and Grizel 1978; Balouet and Poder 1979). In the case of oil spills and selected pollutants, long-term and short-term effects are reported. Programs of depuration of shellfish following exposure to oil have been initiated (Michel 1976).

Contamination of shellfish with heavy metals, pesticides, industrial chemicals (e.g. PCB's) and other toxic substances has become an important public health concern (Goldberg 1975). Although many chemical assays have been conducted, relatively little is known concerning the influence of these substances upon shellfish (Wenzloff et al. 1979; Feng et al. 1978; Bayne 1978; Davis and Pirie 1978; and Barzcz et al. 1978). Since little is known relative to the role of these substances in mass shellfish mortalities, conclusions will have to await further studies. More chronic lesions and mortalities, including neoplastic and degenerative processes, have been attributed to pollutants.

Oceanic dumping, especially from large urban areas such as the New York Bight and other major harbor areas, has been incriminated in massive shellfish mortalities related to pollution (Sindermann 1979).

A variety of shell deforming and reproductive diseases have been associated with copper and organic tin (TBT) toxicities (Alziev 1980). The role of copper in mass mortalities is not known. Considering the nature of the shell lesions associated with TBT, more chronic but persistent mortalities would be expected at natural exposure levels.

8. Neoplasms

Massive mortalities have been attributed to neoplastic processes in a great number of species of shellfish in widely separated geographical areas on many continents (Brown et al. 1976; Christensen et al. 1974; Farley 1976; Mix 1975; and Wolf 1976).

DISCUSSION AND CONCLUSIONS

A review of abnormal mass shellfish mortalities has been presented. Our state of knowledge of the causes of such abnormal mass mortalities is limited but evolving. Much of what we have learned has been the result of continuing studies, converting the unknown to the known by repeated examination, continuing commentaries, and the application of new methods.

As a relatively new science with intrinsic difficulties of dealing with a great variety of species of shellfish in a varied aquatic environment, our progress in shellfish disease research has been slower than our much older sister medical sciences that deal with well known terrestrial animals. Much of what we are doing is research, rather than routine diagnostic work. We cannot identify many etiological agents nor define the pathogenesis of the

diseases they produce. Some of our difficulties relate to problems in dealing with the aquatic environment. Our animals are difficult to observe in natural waters. We cannot easily determine the morbidity and mortalities, or collect representative specimens and grossly examine the animal for lesions of specific organs. In addition, many of our problems rely upon interaction of many classes of organisms, such as we commonly see in the pathology of fouling. We are constantly confronted with problems of predation which are of minor importance in other forms of medicine.

To resolve the problems of abnormal mass mortalities, we will need the collaboration of all of our colleagues, both at home and abroad. Our problems are no longer uniquely localized. We will need to share our information and develop a more universal understanding required to manage our depleting shellfish resources. In our attempts to move from a state of wild shellfish harvest alone to include one of intensified husbandry, new demands are being made to meet the technical challenge. Greater efforts are needed to develop microbiological methods for isolating, identifying and studying disease agents; understand the immune response; understand the physiological response of shellfish to their environments; and understand nutritional pathology and toxicology. Without this knowledge, we cannot prevent, control or eradicate disease.

With the advent of intensified culture systems, we must include all stages of the shellfish life cycle in consideration of mass mortalities and productive efficiency. We must evaluate specific genetic strains for their performance in a given environment, and determine methods for providing the needed optimal environment and nutrition required to obtain maximum economic yields.

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OYSTER SELF-RESISTANCE MECHANISMS TO DISEASES

K. MORI *

RESUME : la prévision et la prévention des mortalités massives des mollusques en élevage passent par un suivi de leur état physiologique. Les méthodes qui sont ici passées en revue concernent la détection et la mesure des réactions de défense de l'hémolymphe (bactéricidines, agglutinines, phagocytes, etc.) ; une liste des hémocytes est dressée, ainsi que de leurs fonctions connues. L'activité de défense est accrue par l'injection d'hétéroantigènes. Le dosage des agglutinines s'est révélé un bon indicateur de l'activite physiologique des huîtres. Il se révèle que des mortalités massives seraient liées à un état de stress : la théorie du stress physiologique est explicitée. Mais le besoin pour des méthodes de culture cellulaire apparaît nettement, tant pour les études fondamentales que pour la caractérisation des souches et l'étude de leur adéquation à l'environnement.

Japan is on all sides surrounded by the sea and the coastline of this island country is very long in proportion to the land area. There are numerous islands of various sizes around the four principal islands. These facts indicate that Japan has extensive coastal waters available for aquaculture. Part of these coastal waters are actually utilized for cultures of seaweeds, bivalve mollusks, fishes, crustaceans, etc. Unlike the seaweed culture the bivalve molluscan culture aims at the production of animal protein for its object, and unlike the finfish or crustacean cultures it falls under the category of the nonfeeding culture which utilizes natural primary production. From the viewpoint of biological economy, therefore, it is one of the most rational methods for the production of animal protein, and hence, in the present-day Japan of the so-called 200 nautical miles era, there seems to be a growing tendency that high productive or industrial value is placed on this bivalve molluscan culture.

The physiological activity in marine bivalve mollusks has been investigated in relation to their energy metabolism mainly during the sexual maturation and spawning, since it is regarded as one of the most fundamental data for analyzing the causative agent of unusual mass mortalities among the mollusks under culture (Mori et al., 1965a; Mori, 1979). The

* Laboratory of Aquacultural Biology, Department of Fishery Science, Faculty of Agriculture, Tohoku University, Sendai 980, Japan

environmental conditions in and around the bivalve molluscan culture area in Japan are not always favorable for their culture and, in addition, there are many problems related to cultural technics awaiting solution, strongly suggesting the possibility that unusual mass mortalities of marine bivalve mollusks may recur frequently in some principal culture areas. Hence, it will become increasingly necessary to forecast the occurrence of such mass mortalities through the daily scientific culture management which requires much accurate information on the physiological activity of the animals under culture and to take preventive measures against the mortalities.

It has been usual for us to assess the physiological activity in such important bivalve mollusks as the oyster, Crassostrea gigas, and the scallop, Patinopecten yessoensis, cultivated in Japan, by judging collectively from the results on the respiratory metabolism of tissues, ciliary activity of gill, glycogen content of whole soft body, and mortality rate (Mori, 1975, 1979). On the other hand, a simpler and preciser means has been desired to be practically used for evaluating the physiological activity.

Mollusks in general have the nonspecific hemolymph defense factors of bactericidins (Cushing et al., 1971; McHenery et al., 1979), agglutinins (Yeaton, 1981a,b), phagocytic capacities (Foley and Cheng, 1975; Cheng, 1983) and so on. Generally, however, the activities of these factors have not been evaluated in the context of the total defensive capacity, i.e., the physiological activity of the animal. In view of the above facts, the presence of these defense-factor activities in C. gigas was first investigated, together with partial characterization of the factors. The experiments in enhancing the defense-factor activities by the injection of heteroantigens

were then carried out to establish whether the so-called immune response can be induced. Finally, the possibility of expressing their physiological activity in terms of a defense-factor value was studied on the basis of the data on the seasonal changes in defense-factor activities.

Occurrence of Defense-Factors and Their Partial Characterization

Agglutinins

Two-year-old oysters, C. gigas, in hanging cultures in Miyagi Prefecture were used in this study. Hemagglutinin activities in oyster tissue extracts, hemolymph, body fluid, tissue fluids and mantle cavity seawater were determined by the Cooke Microtiter System (Cooke Engineering Co., U.S.A.). The extracts of the gill and digestive diverticula exhibited a high level of natural agglutinin activity against sheep red blood cells (SRBC) (Table 1). Lower but considerable activities were found in the extracts of the mantle and adductor muscle. The hemolymph showed a much higher natural agglutinin activity than was observed in the extracts of the gill and digestive diverticula collected at the same time (Table 2). About the same level of activity as found in the pericardial fluid was detectable in the body fluid and tissue fluids (Table 3). In this table, the body fluid-I refers to the fluid oozing out from the adductor muscle injured when the right shell-valve was removed and the body fluid-II stands for the fluid exuding after the operative removal of the gills and mantles, implying that a part of the remaining fluid-I was unavoidably mixed with the fluid-II. The tissue fluids were obtained by centrifuging the minced tissues. In addition to the interior of the soft body, the natural agglutinin titer was detected in the

seawater which was introduced into the oyster mantle cavity, although it was lower than that of the gill or the hemolymph from the animals tested (Fig. 1).

Heat stability of hemagglutinin activity *in vitro* in oyster body fluid-II (Table 3) was investigated and compared with the results of the tissue extracts and hemolymph (Fig. 2). The stability in the body fluid was approximately intermediate between those of the tissue extracts and hemolymph. The low heat stability observed in the tissue extracts is supposed to be due to the denaturation at a relatively low temperature of proteins other than hemagglutinin(s). Comparison of natural hemagglutinin activities in oyster body fluid-II against equine, sheep and human erythrocytes revealed a marked high activity against equine red blood cells (ERBC) (mean agglutinin titer : 973) and much the same activities against three different types of human erythrocytes (Table 4). It is suggested that the hemagglutinins of *C. gigas* body fluid lack human blood group specificity. Agglutinin activities against equine and human erythrocytes disappeared after the addition of EDTA or Na-citrate (Table 5). They were restored by the addition of $CaCl_2$, but $MgCl_2$ had practically no recovering effect, indicating that calcium ions play an important role in the binding of hemagglutinins to these erythrocytes. On the other hand, the activities against sheep erythrocytes were maintained constant even if EDTA or Na-citrate were added. These data are compatible with the results of McDade and Tripp (1967). Heat stability of natural agglutinin activities in the body fluid-II against ERBC and SRBC in the presence of $CaCl_2$, was greatly diminished by the addition of EDTA (Fig. 3), suggesting the possibility that calcium ions are involved in stabilizing the molecular structure of hemagglutinins in

the oyster. In order to examine the pH stability of the oyster natural hemagglutinin activity, SRBC were used as indicator cells, since it was found that the agglutination of SRBC in the body fluid is not affected by the presence or absence of calcium ions (Table 5). The agglutinin activities were measured over a pH range of 6.0 to 9.5 by using three types of buffer solutions (Fig. 4). As a result, it was observed that the activities declined markedly when the pH was changed to the acidic side of physiological pH. The agglutinin titers at the pH below 6.0 were not able to be determined owing to an intense hemolysis of indicator cells.

Cross adsorption tests (Table 6) indicated that oyster hemagglutinin(s) for any type of human erythrocyte employed were completely adsorbed with any type of human erythrocyte, showing the lack of ABO blood-group specificity. However, such a complete adsorption was not found among three different species. This incomplete adsorption was most remarkable between human and equine erythrocytes. None of the saccharides tried inhibited the agglutination of ERBC by oyster body fluid, while N-acetyl-D-glucosamine, N-acetyl-D-galactosamine and N-acetylneuraminic acid (NANA) were specific inhibitors of oyster agglutinins for sheep and human erythrocytes (Table 7). Both porcine gastric mucin (PGM) and bovine submaxillary gland mucin (BSM) were found to inhibit the agglutination of equine, sheep and human erythrocytes by oyster body fluid (Table 8). BSM was more effective in inhibiting the agglutination than PGM. The most striking inhibition by BSM was observed in the agglutination of human erythrocytes. From the results of adsorption experiment (Table 6) and inhibition tests (Tables 7 and 8), it may be concluded that C. gigas has at least 3 types of natural agglutinins which possess their individual binding specificity

for saccharide moieties. It can be assumed that a great inhibition of the agglutinin specific for human erythrocyte by treatment with BSM is due to the fact that BSM is rich in NANA. Hardy et al. (1978) have isolated 7 types of agglutinins from C. gigas hemolymph by affinity chromatography using a Sepharose-BSM column.

Bactericidins

Two-year-old oysters, C. gigas, in hanging cultures were used in this study. The methods for determining the bactericidal activities in bivalve molluscan tissue extracts have been described in our previous reports (Mori et al., 1980a,b). Arthrobacter sp. (HS 29 strain) and Micrococcus luteus were found to be adequate test organisms for the bactericidal activities of the oyster (Table 9). The natural bactericidal activity against HS 29 strain was detectable in the mantle and gill extracts in addition to the extract of digestive diverticula (Table 10). The activity increased with decreasing the pH of the extract of digestive diverticula from 7.0 to 4.0, while it was almost unchanged in the pH range from 7.0 to 10.0 (Fig. 5). In general, the dialysis caused a decrease in the level of bactericidal activity in the pH range tested.

Phagocytic Capacities

The culture medium and the procedure for measuring the phagocytic capacities in two-year-old oysters, C. gigas, are shown in Table 11 and Fig. 6. Formalinized SRBC were phagocytosed by 11% of the oyster amoebocytes in vitro after 60 min incubation at 20°C (Table 12). The maximal phagocytosis was obtained when the SRBC were treated with OHM buffered

to pH 7.0-8.0 (Table 13). The mean percentage of amoebocytes phagocytosing 3 or more erythrocytes was significantly increased when these erythrocytes were pretreated with oyster hemolymph or body fluids (Table 14), suggesting that the humoral factor(s) serving as opsonic substance(s) occurs in the oyster.

Table 15 summarizes the nomenclature and morphological characteristics of blood cells of C. gigas, together with those of C. virginica. Cheng (1981) has been emphasized in his review that although the classification of bivalve hemocytes has been a topic of interest for many years, it has only been recently that some semblance of agreement has evolved ; even then, complete agreement has still not been achieved.

It seems to us that the determination as to how many types of hemocytes occur in oysters is indispensable for the progress of the study on their defense mechanisms. This type of research will become possible through the further development of cell culture techniques. It is clear that we can not classify blood cells precisely by means of the conventional histological method only.

Separation of C. virginica hemocytes by density gradient centrifugation and identification of their surface receptors by employing lectins with different sugar specificities have been tried by Cheng et al. (1980) with a degree of success, suggesting that the subpopulations of the granulocytes distinguishable by their dimensions and densities may be further subdivided by differences in specific surface binding sites. If it becomes feasible to culture each type of hemocytes separately through the establishment of the technical system of separating hemocytes individually, it will become possible to analyze the differences in functional capabilities related particularly to the cellular defense mechanisms among hemocytes at different developmental stages. Although it has been firmly established that the

hemocytes of mollusks comprise the principal line of defense against non-self particulate and soluble materials (Cheng et al., 1980), there is still much left to be studied hereafter about the detailed function of each type of hemocytes.

Experiments in Enhancing the Defense-Factor Activities by the Injection of Heteroantigens

The bactericidal activity in the extract of digestive diverticula from two-year-old oyster, C. gigas, was observed to increase after the injection of formalin-killed HS 29 strain vaccine which was given into the connective tissue surrounding digestive diverticula (dose : 1.8 X 10^8 cells/g fresh soft-body wt.) (Fig. 7) or the adductor muscle (8.3 X 10^5 cells/g fresh soft-body wt.) (Fig. 8). The agglutinin activities in the extracts of oyster digestive diverticula and gill were enhanced by the injection of 0.1 ml/oyster of 10% SRBC suspension into the connective tissue surrounding digestive diverticula (Fig. 9).

In the experiment of Hardy et al. (1977), the hemagglutinin titers of the oyster, C. gigas, were shown to be enhanced by challenge with Vibrio anguillarum. This challenge was given not by injection but by exposure. Two groups of 12 oysters were maintained in tanks of aerated seawater, to one tank was added V. anguillarum (10^6 cells/ml), the other tank acted as control. Three oysters were removed from each tank at intervals of 6, 24, 48 and 140 hrs after the start of experiment. Hemolymph was collected directly from the heart and agglutinin titers were determined. As a result, the oysters in the tank containing the bacteria showed substantially enhanced agglutinin titers. No bacteria could be detected by direct plating of hemo-

lymph taken aseptically from the heart of both experimental and contol oysters. According to them, the failure of other workers (Acton et al., 1969) to enhance agglutinin titers by injection of red blood cells into C. virginica is probably due to two factors. Firstly, red blood cells may be an unnatural challenge if the agglutinins are involved in defense against bacteria. Secondly, injection may be the wrong route by which to challenge the oyster, which is constantly monitoring the particles in the water as a result of its filter feeding habit and the mechanism for triggering agglutinin production may well lie outside the animals' blood system. The above discussion by Hardy et al. has been described assuming that injection of red blood cells is a challenge inappropriate to enhancing the oysters' hemagglutinin titers. The results shown in Fig. 9 indicate that their assumption is not always correct in the case of C. gigas.

Our results (Figs. 7-9) clearly exemplify the induction of higher defense-factor values by contact between the defense system and foreign materials in the marine bivalve mollusk. It is possible that such immune responses may give rise to a danger of overestimating the actual defensive capacity of the animal when the defense-factor value is practically used as a means of evaluating the physiological activity. Hence, it is necessary for us to suspect that heteroantigens have invaded more or less the animal when an unusually high defense-factor value is obtained during a series of immunological tests for the physiological activity.

Possibility of Expressing the Physiological Activity in Terms of a Defense-Factor Value

Several long-term experiments were performed to ascertain whether

there is a seasonal relationship between the so-called physiological activity (Mori et al., 1965a,b; Mori, 1979) and the defense-factor activities in the oyster, C. gigas, under culture.

It is well known that the physiological activity in the oyster in hanging cultures declines with progressive development of the gonads and is minimal at spawning (Mori, et al., 1965a). The natural agglutinin activities in the extracts of gill and digestive diverticula declined as sexual maturation proceeded, and fell to a minimum level just before and during the spawning (Fig. 10), paralleling the declines in the physiological activity of the animal. On the other hand, there was no seasonal relationship between the natural bactericidal activity of oyster digestive diverticula (Fig. 11) and the physiological activity. In addition, variations in bactericidal activity between individual members were found to be generally considerable, suggesting that the sensitivity of test bacteria for bactericidal activity is not always stable enough to ensure a constant use of them (Fig. 11).

The present study has revealed that the natural agglutinin(s) is the effectual defense-factor as a practical means of evaluating the physiological activity in the oyster. However, the bactericidal value is not available for practical use as an indicator for the physiological activity unless a constant use of bactericidal test bacteria showing stable sensitivity is ensured.

So-called "Physiological Stress Theory" and Main Subjects to be Investigated Hereafter on a Worldwide Scale

To summarize the results of various investigations on the large-scale deaths of oysters, C. gigas, that have often recurred in some of the important oyster culture areas in Japan, particularly but not exclusively on the Pacific Ocean coast and the Inland Sea, most of these mass mortalities have not been ascribed to epizootics caused by infectious agents: specific pathogens are not considered by us to be primary causes of mass mortalities in Japan (Imai et al., 1968, 1965; Kan-no et al., 1965; Koganezawa, 1975; Mori, 1979; Mori et al., 1965a,b; Numachi et al., 1965; Sindermann, 1979; Tamate et al., 1965). On the other hand, Glude (1975) emphasized the striking similarities between C. gigas mortalities in Matsushima Bay, Japan, and those in Puget Sound (Washington) on the United States Pacific coast. In both places, as he points out: (1) fast-growing oysters died, (2) affected oysters were characterized by rapid over-maturation of gonads, (3) mortalities occurred during the summer spawning period, and (4) no specific pathogen could be associated with the mortalities, despite indications of degenerative necrosis of the digestive diverticula. C. gigas at that time was largely imported as seed from Japan and planted in waters of the west coast states of Washington, Oregon and California. Since no clear association, however, has been made of specific pathogens with mortalities of C. gigas on the Pacific coasts of Japan and the United States as described above, it is quite possible that other environmental factors were operative in the mortality areas. According to Sindermann (1979), one of Glude's conclusions is that "The failure of pathological investigations to find a causative organism tends to strengthen the physiological stress theory" (introduced and discussed in the above Sindermann's paper as Mori's hypothesis to account for Matsushima Bay mortalities).

The hypothesis is based on overmaturation of the gonad under the influence of high temperatures and eutrophication of growing areas, disturbance of lipid and steroid metabolism, extreme decline in physiological activity, and death (Mori et al., 1965a,b; Mori, 1979). This hypothesis was built up under the guidance of the late Professor T. Imai, Tohoku University, Sendai, Japan.

Even though the failure of many pathological investigations to recognize specific pathogens tends to strengthen our "physiological stress theory" as Sindermann points out, it can not be denied that oysters are liable to such an infection or disease as might possibly lead to their death, when physiologically inactive ones happen to encounter a bacterial or parasitic pathogen at its strong stage of pathogenicity. If, however, oysters are in the high stage of physiological activity or the virulence of the pathogen that they encounter is weak even in the low stage of their physiological activity, the possibility that they suffer from infectious disease will get small even in an infective environment. In brief, the question is the relationship between the power of vital resistance of oysters and the strength of virulence of causative organisms, and infection does not always lead to disease. It is necessary, therefore, to investigate seasonally and chronologically the relationship between the defensive capacity of oysters and the pathogenicity of suspectable pathogens in the principal oyster-culture areas of the world. In order to make such important investigations feasible, it is preferable to establish the culture technique of producing the oyster tissue-culture cells which contain a certain quantity of known defense factor and retain a fixed defensive capacity. At the same time, it is also desired to establish the technique of culturing successively the suspectable pathogen which contains a certain quantity

of known antigen and show a fixed strength of pathogenicity. If such tissue-culture cells and pathogen are provided as the internationally common indicator cells and organism for test, it will become possible to carry out both fundamental and practical studies of oyster mass mortalities on a worldwide scale.

In an environment, there should be oyster species or race best fitted to it from the viewpoint of the vital resistance to disease or the growth rate. For the purpose of selecting such a species or race, it is advisable to determine quantitatively the total defensive capacity of each oyster in its culture area. Problems such as how to modify the culture technique according to the total defensive capacity are also necessary studies. In addition, since even the same species or race of oysters may possibly show different defensive capacities in different environments, it is hoped that cooperations in the related countries will become closer to compare the same species or race of oysters from different oyster-culture areas of the world in defensive capacity. Such comparative studies, which will be facilitated by oyster geneticists, seem to provide much useful information on the possibility of introducing a new species or race of oyster from abroad.

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Table 1. Hemagglutinin activities in oyster tissue extracts (May 1979)

Tissue	Hemagglutinin titer
Digestive diverticula	128.0 ± 35.0
Gill	140.8 ± 31.2
Mantle	89.6 ± 15.7
Adductor muscle	41.6 ± 9.6

1% sheep red blood cells (SRBC) were used as indicator cells. Means and standard errors on 5 oysters are shown.
From Mori et al. (1980 b).

Table 2. Hemagglutinin activities in oyster hemolymph, gill and D.d.* (Dec. 1980)

Origin	Hemagglutinin titer
Hemolymph	304.0 ± 60.3 (16)
Gill extract	80.0 ± 10.1 (16)
D. d. extract	32.4 ± 8.5 (9)

* Digestive diverticula
1.5% SRBC were used as indicator cells. Means and standard errors (number of oysters) are shown.
From Mori et al., unpublished.

Table 3. Agglutinin activity in body fluid and tissue fluids of oyster (Dec. 1981)

	Agglutinin titer[*1]	
	Range	Mean[*2] ± S.E.
Pericardial fluid	32 - 256	124.5 ± 34.7
Body fluid -I	32 - 256	120.0 ± 22.7
Body fluid -II	32 - 512	147.9 ± 70.0
Gill fluid	32 - 512	152.1 ± 68.7
Mantle fluid	32 - 512	188.4 ± 63.5
D. d.[*3] fluid	16 - 256	90.9 ± 42.8

*1. 2% SRBC were used as indicator cells.

*2. Means and standard errors on 9 samples are shown.

*3. Digestive diverticula.

From Mori et al., unpublished.

Table 4. Hemagglutinin activity in oyster body fluid against equine, sheep and human erythrocytes

Type of erythrocyte	Hemagglutinin titer
	Mean ± S.E.
Equine	972.8 ± 307.2
Sheep	128.0 ± 35.0
Human(A)	83.2 ± 19.2
Human(B)	65.6 ± 27.7
Human(O)	76.7 ± 21.7

2%(v/v) erythrocytes were used as indicator cells.
N = 7
From Mori et al., unpublished.

Table 5. Effect of divalent cations on hemagglutinin activity in oyster body fluid

Two-fold dilution with TBS containing :	Hemagglutinin titer		
	Type of erythrocyte		
	Equine	Sheep	Human(O)
10 mM $CaCl_2$	1024	128	64
10 mM $MgCl_2$	256	128	64
20 mM EDTA	<2	128	<2
20 mM Na-citrate	<2	128	<2
20 mM EDTA, 30mM $CaCl_2$	1024	128	64
20 mM EDTA, 30mM $MgCl_2$	<2	128	<2

TBS : Tris-HCl (pH 8.0) containing 150 mM NaCl.
2 %(v/v) erythrocytes were used as indicator cells.
From Mori et al., unpublished.

Table 6. Hemagglutinin titers of oyster body fluid before and after adsorption with equine, human and sheep erythrocytes

Adsorbed with erythrocyte of:	Hemagglutinin titer				
	Type of erythrocyte				
	Equine	Sheep	Human(A)	Human(B)	Human(O)
Equine	0	32	128	64	128
Sheep	8	0	16	16	16
Human (A)	1024	8	0	0	0
Human (B)	512	16	0	0	0
Human (O)	512	16	0	0	0
Unadsorbed	1024	128	128	128	128

2 %(v/v) erythrocytes were used as indicator cells.
From Mori et al., unpublished.

Table 7. Effects of saccharides on hemagglutinin activity in vitro of oyster body fluid

Saccharide added	conc. (mM)	Hemagglutinin titer Type of erythrocyte		
		Equine	Sheep	Human(O)
D(+)-Glucose	500	1024	256	128
D(+)-Galactose	500	1024	256	128
D(+)-Mannose	500	1024	256	128
D(+)-Xylose	500	1024	256	128
L(−)-Fucose	500	1024	256	128
D(+)-Glucosamine	500	1024	256	128
D(+)-Galactosamine	500	1024	256	128
N-Acetyl-D-glucosamine	500	1024	32	4
N-Acetyl-D-galactosamine	100	1024	64	16
N-Acetylneuraminic acid	100	1024	64	4
None	-	1024	256	128

2%(v/v) erythrocytes were used as indicator cells.
From Mori et al., unpublished.

Table 8. Effects of PGM[*1] and BSM[*2] on hemagglutinin titer of oyster body fluid

Mucin - Conc. (μg/ml)	Hemagglutinin titer Type of erythrocyte		
	Equine	Sheep	Human(O)
PGM — 10	1024	256	128
— 50	1024	256	128
—100	1024	256	32
—200	512	128	16
BSM — 1	1024	256	8
— 5	1024	256	2
— 10	1024	128	<2
— 50	512	128	<2
—100	256	64	<2
None -	1024	256	128

*1. Porcine gastric mucin.
*2. Bovine submaxillary gland mucin.
2%(v/v) erythrocytes were used as indicator cells.
From Mori et al., unpublished.

Table 9. Natural bactericidal activity in the extract of oyster digestive diverticula against test bacteria (Jan. to Feb. 1981).

Test bacteria	Bactericidin titer*
Arthrobacter sp. HS 29 strain	352 ± 175 (5)
A. citreus IFO 12957	37 ± 13 (6)
A. globiformis IFO 12136	0 (5)
Micrococcus luteus IFO 3333	284 ± 86 (9)
Escherichia coli NIHJ	0 (5)

* Reciprocal of dilution killing 50 % of bacteria in 90 min at 20 °C (per gram of original tissue).
Averages and standard deviations are presented.
Sample number is in parentheses.
From Mori et al., unpublished.

Table 10. Bactericidal activities in the oyster tissue extracts (May, 1979).

Tissue	Bactericidin titer*
Digestive diverticula	231.1 ± 36.3 (9)
Gill	16.4 ± 3.5 (9)
Mantle	32.5 ± 7.5 (8)
Adductor muscle	0 (6)

*Averages and standard errors (number of oysters) are shown.
Arthrobacter sp. (HS 29 strain) were used as test bacteria.
From Mori et al. (1980 b).

Table 11. Composition of oyster hemolymph medium (OHM)

Constituent	g/liter
NaCl	27.0
KCl	0.7
$CaCl_2$	1.2
$MgCl_2 \cdot 6H_2O$	4.6
$NaHCO_3$	0.5
Na_2HPO_4	0.01
Glucose	1.0
Phenol red(0.4%)	1 ml/liter

Adjust to pH 8.0 with 1 N HCl.

From Nakamura et al., unpublished.

Table 12. Phagocytosis of formalinized sheep erythrocytes by oyster amoebocytes in vitro: Time course change

	Incubation time (min) at 20°C			
	15	30	60	90
% amoebocytes showing phagocytosis ± SE	4.9 ± 0.6	7.5 ± 1.2	11.4 ± 1.1	10.0 ± 0.9
% of phagocytic amoebocytes containing:				
1 erythrocyte	87.2	85.8	83.0	91.5
2 erythrocytes	8.7	9.7	13.8	7.7
≧ 3 erythrocytes	4.1	4.1	3.2	0.9

From Nakamura et al., unpublished.

Table 13. Phagocytosis of formalinized sheep erythrocytes by oyster amoebocytes in vitro : Effect of pH

	pH				
	5.0	6.0	7.0	8.0	9.0
% amoebocytes showing phagocytosis ± SE[a]	3.0 ± 0.3	3.8 ± 0.1	5.3 ± 0.6	5.5 ± 0.6	3.2 ± 0.1
% of phagocytic amoebocytes containing :					
1 erythrocyte	100	100	96.2	88.5	96.4
2 erythrocytes	0	0	3.8	10.7	0
≥ 3 erythrocytes	0	0	0	0.8	3.6

[a] Incubation for phagocytosis : 30 min at 20°C.

From Nakamura et al., unpublished.

Table 14. Phagocytosis of formalinized sheep erythrocytes by oyster amoebocytes in vitro. Effect of treatment with humoral factors

Treatment of sheep erythrocytes with :	% amobocytes showing phagocytosis ± SE	% of phagocytic amoebocytes containing :		
		1 erythrocyte	2 erythrocytes	≧ 3 erythrocytes
Hemolymph	11.5 ± 0.6	52.4	25.1	22.5
Pericardial fluid	9.3 ± 0.5	55.6	18.3	26.1
Body cavity fluid	7.3 ± 0.6	28.8	17.4	53.7
Control (OHM)	9.3 ± 0.3	76.0	18.0	6.0

From Nakamura et al., unpublished.

Table 15. Nomenclature and morphological characteristics of oyster blood cells

Oyster species	Designations of blood cells	Cell types	Dimensions (μm)	Morphological characteristics	Reference
Crassostrea gigas	Blood-corpuscle	12 types	2.0-70.2 (diameter)	Refer to Table 1 of the original report for details	Tanaka et al. (1961)
	Amoebocyte	3 types:	ND*		Ruddell (1971a,b)
		1) Acidophilic granular amoebocyte		Small, spherical, amorphous and osmiophilic cytoplasmic granules (0.4-0.56 μm)	
		2) Basophilic granular amoebocyte		Large round or oval cytoplasmic granules (0.7-1.2 μm)	
		3) Agranular amoebocyte		Torpedo-shaped and monocyte-type cell in wound plug	
	Amoebocyte	3 types:	ND		Feng et al. (1977)
		1) Type I amoebocyte		Small basophilic nucleus (3-5 μm); granular or agranular cytoplasm	
		2) Type II amoebocyte		Neutrophilic nucleus (5-8 μm); granular or agranular cytoplasm	
		3) Type III amoebocyte		Large eosinophilic nucleus (6-10 μm); large amount of granular or agranular cytoplasm	
Crassostrea virginica	Blood-corpuscle	2 types:			Galtsoff (1964)
		1) Hyaline cell	5-15 (diameter)	Spherical; distinct cell membrane; few granules	
		2) Granular cell (amoebocyte)	6 (diameter, contracted)	Amorphous; bristle pseudopodia; neutrophilic or basophilic granules	
	Amoebocyte	8 types:			Tripp et al. (1966)
		1) 1 series (4 types)	8-20 (long)	Small oval nucleus (4.5 x 6 μm); granular or agranular cytoplasm	
		2) 2 series (4 types)	13-80 (long)	Large, round or oval nucleus (6-10 μm, long); granular or agranular cytoplasm	
	Leucocyte	4 types:			Feng et al. (1971)
		1) Granular leucocyte	10-20 (diameter)	Round or oval-shaped nucleus; cytoplasm with light or dense granules	
		2) Agranular leucocyte	8 (diameter)		
		Type I		Lymphocyte-like cell; large oval nucleus; scanty cytoplasm	
		Type II		Oval nucleus; large cytoplasm	
		Type III		Spherical nucleus with dense chromatin; numerous vesicles	
	Hemolymph cell	2 types:			Cheng (1975, 1983)
		1) Granulocyte	13±1 x 12±1.2 (fresh)	Acidophilic, basophilic and refractile granules	
		2) Hyalinocyte	9.3 x 8.2	Scanty cytoplasm with none or few granules	

*not described.

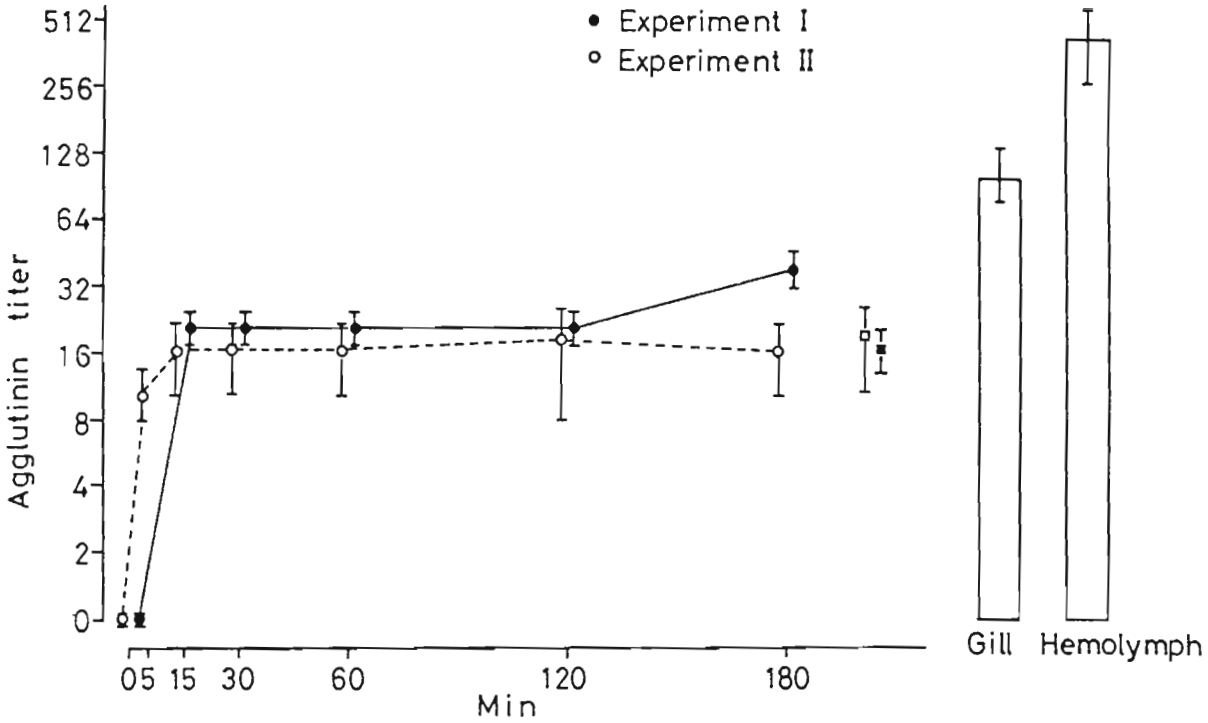

Fig. 1. Natural agglutinin activity of sterile seawater after being introduced into the oyster mantle cavity (Feb., 1981). Sterile seawater (5ml) was introduced into the mantle cavity and 0.4ml was collected each time interval (0.4ml of sterile seawater was added to the mantle cavity after each sampling). The squares (■,□) represent the titers of the total volume of 5ml after 180min. The agglutinin titers of the gill and hemolymph from the tested animals in Experiment I are shown on the right. 1% SRBC were used as indicator cells.
From Mori et al., unpublished.

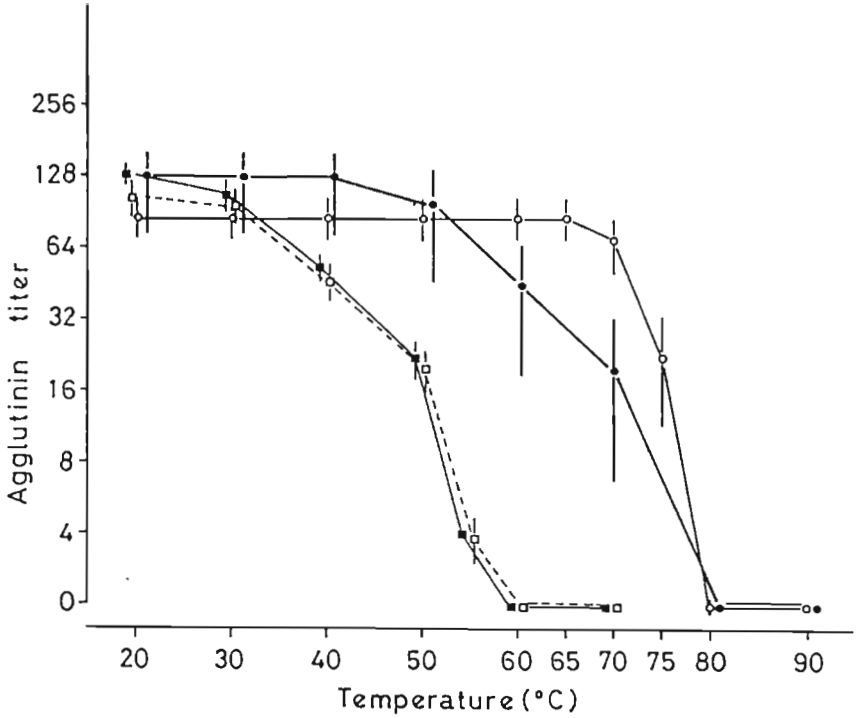

Fig. 2. Heat stability of hemagglutinin activity in vitro in oyster body fluid (Feb. 1982)
2% SRBC were used as indicator cells. Each point (•) indicates the mean value for individual determinations on 5 samples (± standard error). Heat stability of hemagglutinin activities in vitro of the gill (■) and digestive diverticula (□) extracts (Mori et al. 1980) and the hemolymph (○) (Mori et al., unpublished) is also presented.
From Mori et al., unpublished.

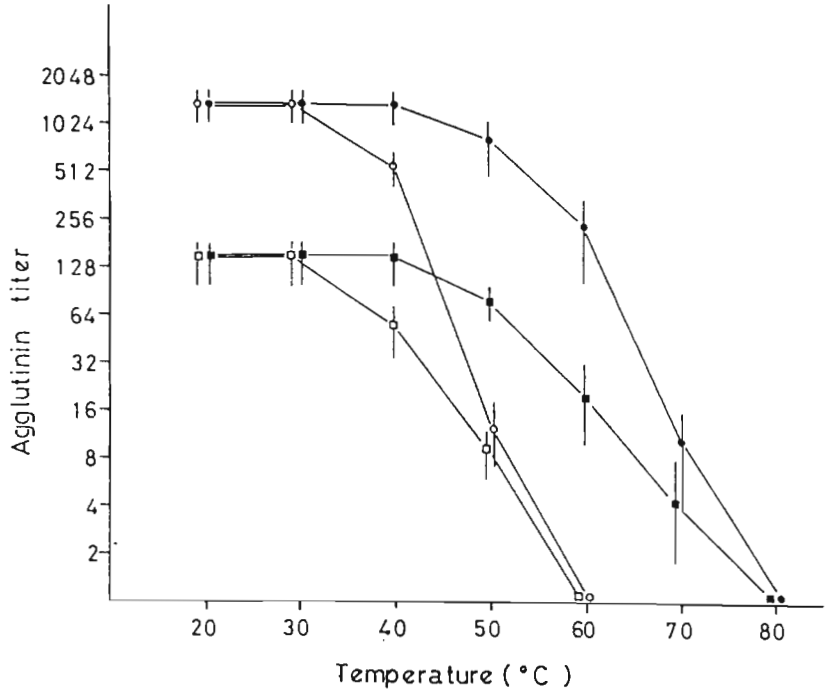

Fig. 3. Effects of divalent cations on heat stability of agglutinin activities in oyster body fluid (Feb. 1982). Samples were added the equal volume of TBS/10mM $CaCl_2$ (pH 8.0) or TBS/20mM EDTA (pH 8.0), incubated and heated at each temperature for 30 min. For the hemagglutinin assay, 2% SRBC and ERBC were used as indicator cells. Each point represents the mean value (± standard error) on 5 samples.

- ●——● plus TBS-10mM $CaCl_2$ with ERBC
- ○——○ plus TBS-20mM EDTA with ERBC
- ■——■ plus TBS-10mM $CaCl_2$ with SRBC
- □——□ plus TBS-20mM EDTA with SRBC

From Mori et al., unpublished.

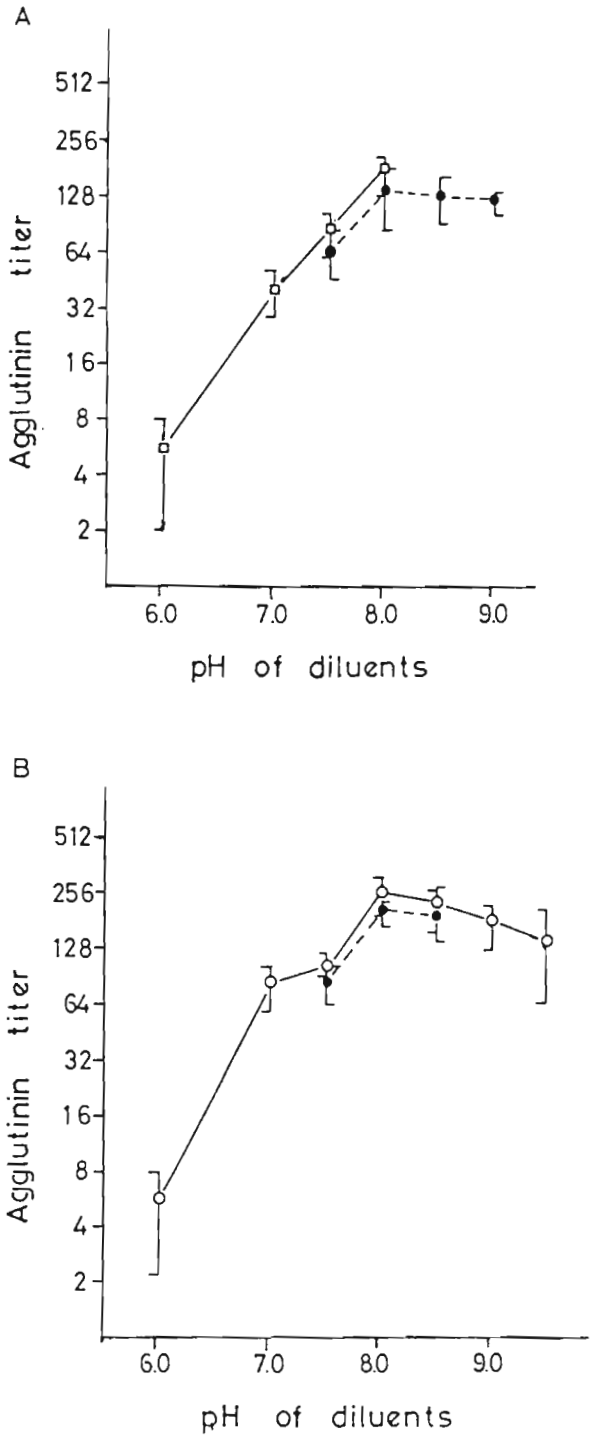

Fig. 4. Effects of pH on hemagglutinin activity of oyster body fluid (Aug. 1981). Samples were titrated using the following diluents;

A; TBS (50mM Tris-HCl, 150mM NaCl) pH 7.5-9.0 •·····•

KBS (50mM KH_2PO_4-50mM Na_2HPO_4, 150mM NaCl) pH 6.0-8.0 □——□

B; TBS pH 7.5-8.5 •·····•

UBS (Britton-Robinson buffer, 150mM NaCl) pH 6.0-9.5 ○——○

2% SRBC were used as indicator cells, and suspended in the same buffer used as diluents. Each point represents the mean value (± standard error) on 5 samples. From Mori et al., unpublished.

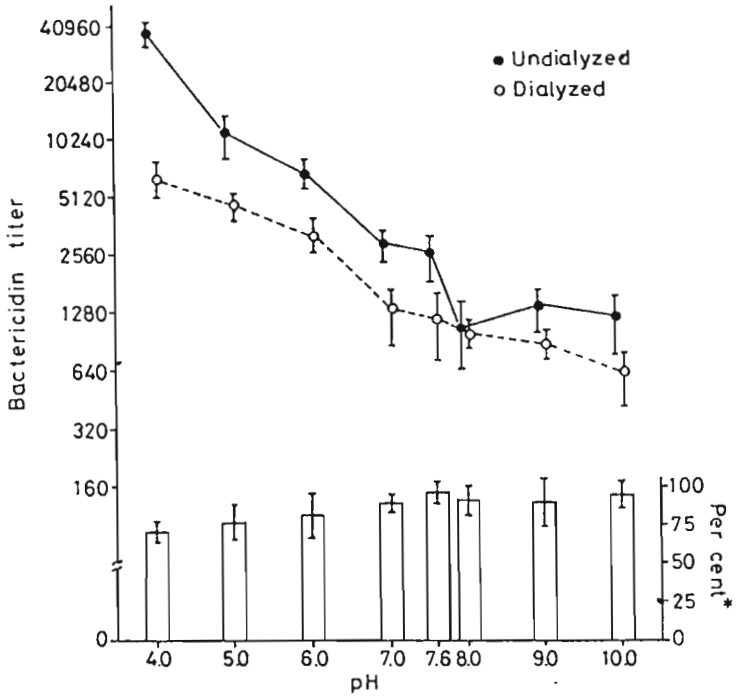

Fig. 5. Effects of pH on the natural bactericidal activity in vitro of oyster digestive diverticula against Arthrobacter sp. HS 29 strain. Each point indicates the mean value for individual determinations on 5 samples (± standard error).

* Survival rate of HS 29 strain after incubating at each pH value for 90 min.

From Mori et al., unpublished.

Collection of hemolymph from the ventricle of oyster with a tuberculin syringe

↓

25 µl of hemolymph to a coverslip

↓

Preincubation in humidified chamber for 45 min

↓

Addition of 25 µl of 5% sheep erythrocytes(formalinized) in OHM

↓

Incubation for phagocytosis

↓

Washing with 125 µl of OHM

↓

Fixation in MeOH for 5 min

↓

Drying in the air

↓

Staining with May-Grünwald's solution for 10 min

↓

Staining with Giemsa's solution for 60 min

↓

Washing with OHM and D.W.

↓

Drying in the air

↓

Microscopy

Fig. 6. Outline of the method for measuring the phagocytosis of sheep erythrocytes by oyster amoebocytes in vitro. (From Nakamura et al., unpublished.)

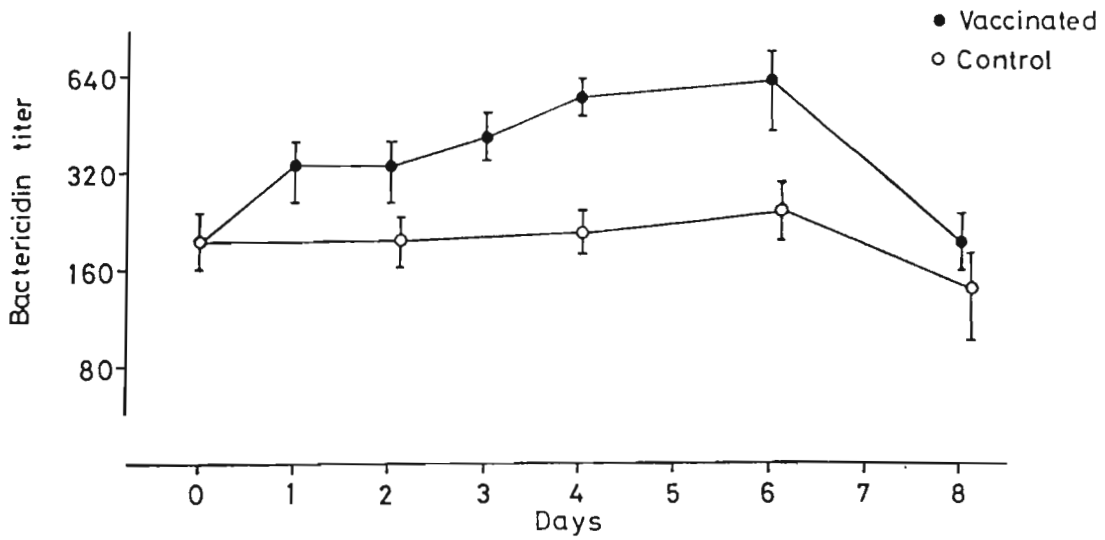

Fig. 7. Changes in the bactericidal activities of oyster digestive diverticula against HS 29 strain with time after injection of HS 29 strain vaccine (Dec., 1979). The vaccine was injected into the connective tissue surrounding digestive diverticula. Each point represents the mean value for individual determinations on 5 oysters (± standard error). From Mori et al. (1980 b).

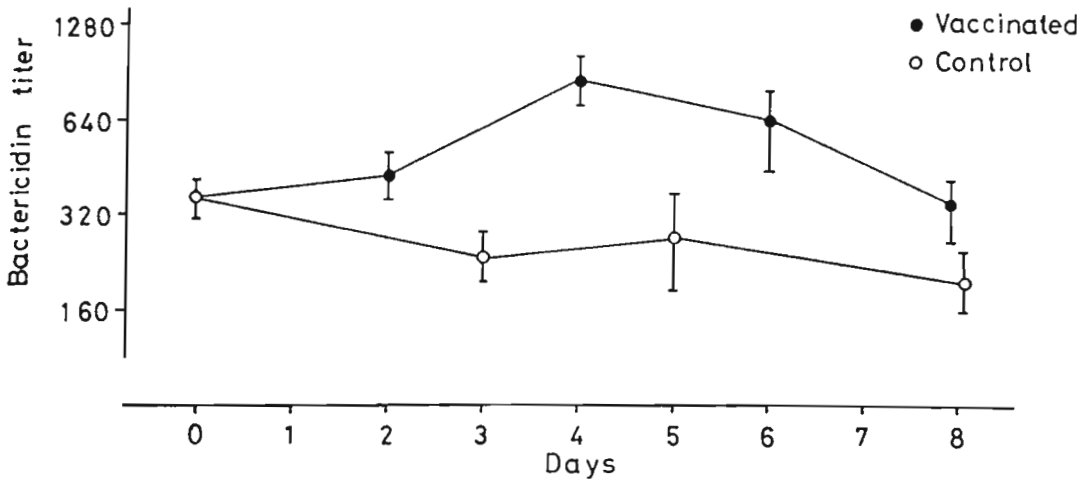

Fig. 8. Changes in the bactericidal activities of oyster digestive diverticula against HS 29 strain with time after injection of HS 29 strain vaccine (Feb., 1980). The vaccine was injected into adductor muscle. Each point represents the mean value for individual determinations on 5 oysters (± standard error). From Mori et al. (1980 b).

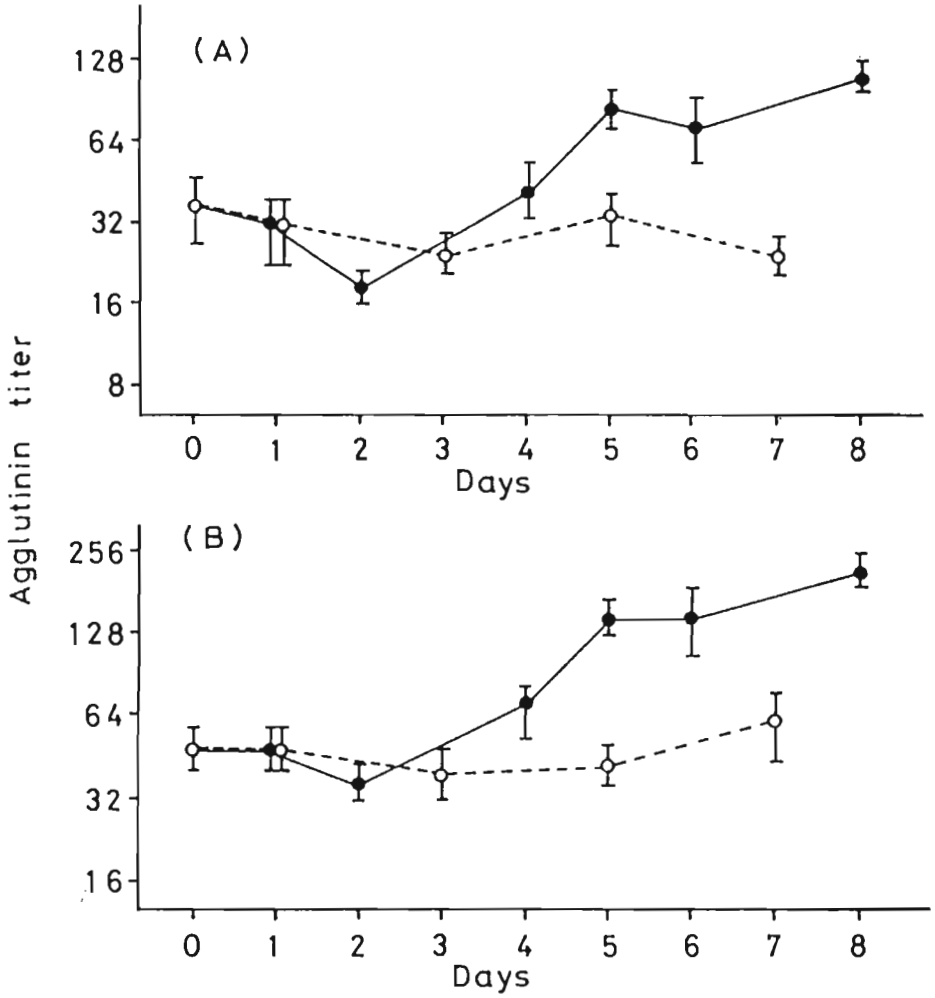

Fig. 9. Changes in the agglutinin activity of oyster digestive diverticula and gill against 1 % SRBC with time after injection of 0.1 ml/oyster of 10 % SRBC (Feb., 1980). The cells were injected into the connective tissue surrounding digestive diverticula. Each point represents the mean value for individual determinations on 5 oysters (± standard error). (A): digestive diverticula ; (B): gill ; • : SRBC-injected group ; o : control group.
From Mori et al. (1980 b).

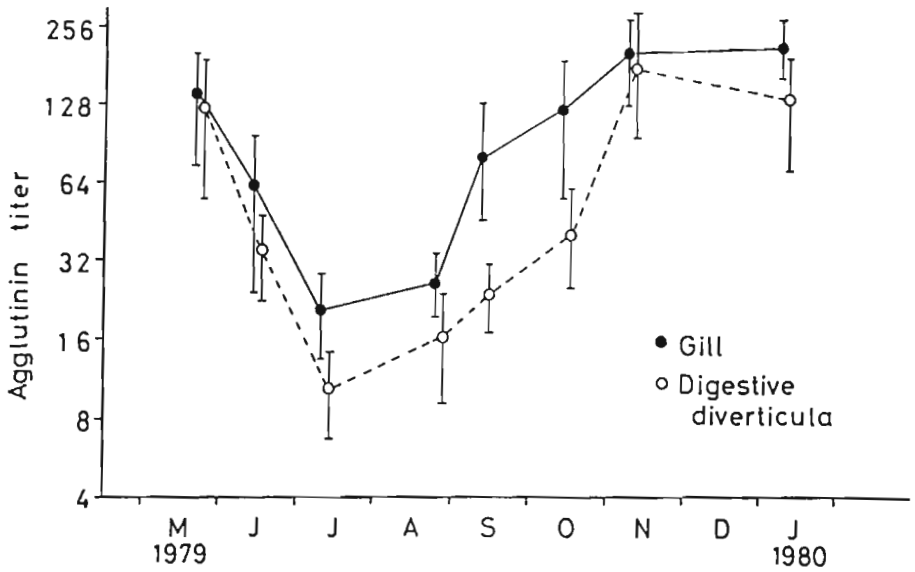

Fig.10. Seasonal changes in the natural agglutinin activity of oyster digestive diverticula and gill against 1 % SRBC (May, 1979 to Feb., 1980). Each point represents the mean value for individual determinations on 5 oysters (± standard deviation). From Mori et al.(1980 b).

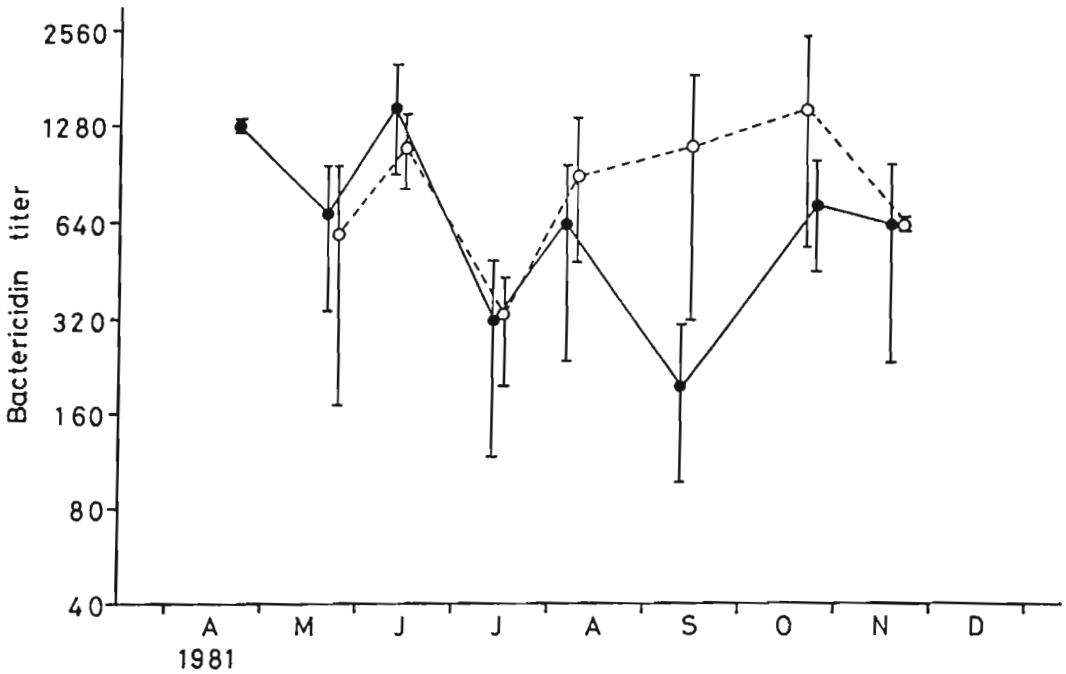

Fig.11. Seasonal changes in the natural bactericidal activity of oyster digestive diverticula. Each point represents the mean value for individual determinations on 5 oysters (± standard deviation). ○ : tested against Arthrobacter sp. HS 29 strain ; • : tested against Micrococcus luteus.
From Mori et al., unpublished.

GENETICS

GENETIQUE

SUMMARY OF GENETICS SESSION

B. CHEVASSUS *

The primary purpose of this session was to assess the value of different genetical techniques for enhancing shellfish production.

I. Enzyme polymorphisms

In general, electrophoretic estimates of genetic diversity can be made at 4 integrational levels.

I.1. Taxonomical level

The risks linked to an erroneous definition of species have been underlined. These are potential reduction of fertility and viability of F_1 and F_2 animals but are hypothetical in the case of molluscs. Biochemical genetics could be used to assess the biological status of supposed sibling species (There should also be a quantitative analysis of F_1 and F_2 within population crosses performances before the promotion of a global management programm implying exchange and crossing among sub-units).

I.2. Interpopulation level

The intrinsic value of electrophoretic data for the management of wild shellfish resources has been underlined. Allele frequencies can provide inferences on the degree of reproductive isolation among populations thus allowing the estimation of genetic flow and differentiation.

It was pointed out however that the value of this information for production improvement is limited. For example, populations considered homogenous by electrophoresis can be shown to have significant levels of heritable morphological variation.

I.3. Intrapopulation level

Mean heterozygosity appears to be a useful parameter to follow the genetic changes (reduction) in closed populations or to estimate the potential response for selection (etimation of initial genetic variability). Little information is currently available.

I.4. Interindividual level

Several examples of correlations between levels of heterozygosity and production characters for several bivalves species have been documented. On the surface this would appear a useful approach for production improvement. Doubts were however expressed on its usefulness based on the following :
(1) The associations seem to disappear in cultured populations

* INRA, Département d'Hydrobiologie, 78350 **Jouy-en-Josas**, France

(2) The strengh of the association is at an optimum with young animals and tends to zero with increasing age
(3) less than 1% of the total phenotypic variance can be explained by heterozygosity.

II Quantitative genetics

Several methods for the enhancement of production have been reviewed.

II.1. Assessment of population performance

This evaluation is based on the analysis of animals either from wild sources or pure population matings when grown in common environments. Its is a short term improvement approach but can still provide substantial gain. Testing should be made on large scale to have a commercial value and should be coordinated with other disciplines (e.g. testing of new technologies).

II.2. Selective breeding

Only very few quantitative genetics studies have been conducted on molluscan shellfish. Therefore, it remains difficult to appraise the likely success of selection progress. Reasons must be limited facilities for such work, lack of integrated genetic and hatchery programs, and the general difficulty of properly controlling these studies adding to their costs. However, just about all attemped selection experiments have produced substantial production improvement. Experiments should be proposed for estimating selection response and heritability estimates for a number of economic characters (growth, disease resistance, conformation, metabolic efficiency). Family selection combined with individual selection should be considered to prevent undesirable negative correlated changes.

II.3. Hybridization and heterosis

Little is known about the value of crossing natural populations for commercial improvement. We know however that populations indigenous to certain estuaries are not necessarily those that grow the fastest. These studies should be developed and integrated with the program of population evaluation (II.1). Also, interspecies crosses of some shellfish species could be of direct use in commercial production, and as founding stock for selection programs, and ought to be further exploited.

III. Cytogenetics

As classic cytogenetics interfaces with molecular biology and use of recombinant DNA technology is limited by inadequate information on the role of chromosomes as gene regulators, there is a strong resurgence of interest in all aspects of chromosomes. This has resulted in exciting new information and powerful new technology. All of this is bound to influence views on natural genetic variability, and how selection programs are conducted, possibly with very considerable advantage to shellfish culture. A large bibliography is given with up-to-date references providing useful information on the current state of cytogenetics and its latest methods.

Chromosome alterations are important in evolution, and may be essential to the development of shellfish strains more amenable to profitable culture under controlled hatchery conditions. Chromosome engineering can be used to make triploids of perchaps direct use in production of molluscan shellfish. The general nature of polyploids was reviewed, as was agriculture experience with them. Beyond production of triploids, chromosome manipulation can be used to transfer chromosome segments, genes or chromosome between species and strains when a non-commercial form carries a desirable trait, as for disease resistance, absent in the commercial type. By combining polyploidy and hybrization, chances of developing parthenogenetic clones of non-inbred molluscan shellfish of outstanding commercial gene type are probably optimized. Chromosome engineering can also be used to develop homozygous lines for basic research and for crossbreeding, and other shellfish of research interest, as diploid embryos from tetraploid oocytes.

RÉSUMÉ DE LA SESSION GÉNÉTIQUE

B. CHEVASSUS *

L'intention première de cette session est d'évaluer l'apport des différentes techniques de génétique pour accroître la production de mollusques.

I Polymorphismes enzymatiques

En général, l'estimation de la diversité génétique peut être faite à quatre niveaux.

I.1. Taxonomique

Les risques liés à une définition énoncée de l'espèce ont été soulignés. Ils concernent, chez les animaux, une réduction potentielle de fertilité et de viabilité des lignées F_1 et F_2 ; mais ces risques sont hypothétiques dans le cas des mollusques. La génétique biochimique pourrait être utilisée pour établir le statut biologique d'espèces supposées de même origine. Elle pourrait, aussi, être une méthode d'analyse quantitative des performances des lignées F_1 et F_2 résultant de croisement intrapopulation, avant la réalisation d'un programme complet comprenant des échanges et des croisements entre des sous-unités.

I.2 Interpopulation

La valeur intrinsèque des données électrophorétiques pour la gestion des stocks de mollusques a été soulignée Les fréquences alléliques peuvent fournir des inférences sur le degré d'isolement génique des populations, permettant ainsi une estimation des flux génétiques et des différenciations.

I.3. Intrapopulation

L'heterozygotie moyenne apparaît être un paramètre utile pour suivre les variations génétiques (essentiellement réduction) dans une population isolée, ou pour estimer le potentiel de réponse pour une sélection (estimation de la variabilité génétique initiale). Peu d'informations sont actuellement disponibles.

I.4. Interindividus

Deux exemples de corrélations entre le niveau d'héterozygotie et des caractères particuliers ont eté fournis chez plusieurs espèces de mollusques bivalves. A première vue, ceci semblerait être une approche très intéressante pour améliorer la production. Cependant les remarques suivantes permettent d'émettre des réserves sur l'exploitation de ces résultats :

(1) les associations semblent disparaître dans les populations cultivées,
(2) l'intensité des associations est optimale chez les jeunes animaux et disparaît avec l'âge.
(3) moins d'1 % de la variance totale du phénotype peut être expliquée par l'hétérozygotie moyenne.

II Génétique quantitative

Plusieurs méthodes ont été examinées pour accroître la production.

* INRA, Département d'Hydrobiologie, 78350 **Jouy-en-Josas**, France

II.1 Estimation des performances des populations

Cette évaluation est basée sur l'analyse d'animaux issus, soit de populations naturelles, soit de souches pures et élevées dans un environnement commun. Cette approche d'amélioration, bien qu'étant à court terme, peut néanmoins apporter un gain substantiel. Le testage pourrait être effectué à une grande échelle pour vérifier la rentabilité commerciale et pourrait être coordonné avec d'autres disciplines (ex : test de nouvelles technologies).

II.2 Sélection de souches

Peu d'études de génétique quantitative ont été entreprises chez les mollusques. En conséquence il paraît difficile d'évaluer le succès de plans de sélection. Ceci est du au manque d'installation adéquates, à l'absence de programmes intégrés entre la génétique et les écloseries, et aux difficultés générales pour contrôler les expériences sur le terrain et à leur coût. Cependant jusqu'à présent toutes les expériences de sélection ont fourni une amélioration substantielle. Des expériences devraient être faites pour estimer la réponse a la sélection et l'héritabilité d'un certain nombre de caractères économiquement intéressants (croissance, résistance aux maladies, conformation, métabolisme). Une sélection familiale combinée à une sélection individuelle devrait être envisagée pour empêcher des effets secondaires indésirables.

II.3 Hybridation et hétérosis

Peu d'informations sont connues sur l'amélioration obtenue à partir de populations naturelles. Cependant, nous savons que les populations indigènes de certains estuaires ne sont pas forcément les plus performantes. Ces études devraient être developpées et intégrées aux programmes d'évaluation des stocks (II.1). L'hybridation de quelques mollusques pourrait être aussi une méthode utilisable directement en production commerciale. Elle pourrait également servir à créer des lignées exploitables ultérieurement pour des programmes de sélection.

III Cytogénétique

La cytogénétique classique et la biologie moléculaire ont des champs communs et l'usage des techniques de manipulation de l'ADN est limité par un manque d'information sur le rôle des gênes régulateurs ; il y a un fort regain d'intérêt sur les chromosomes. Ceci a créé des informations nouvelles passionantes et une technologie nouvelle puissante.

Les modifications attendues sont succeptibles d'avoir des répercussions sur la compréhension de la variabilité génétique et la conduite de programmes de sélection. Une bibliographie importante est fournie avec une mise à jour des références ; elle donne d'intéressantes informations sur l'état actuel de la cytogénétique et sur les dernières méthodes.

Les altérations chromosomiques sont importantes dans l'évolution et pourraient être essentielles pour la création de lignées plus performantes, maintenues et contrôlées en écloseries. Les manipulations chromosomiques peuvent être utilisées pour obtenir des mollusques triploïdes susceptibles d'être directement élevés. Les caractéristiques générale des polyploïdes sont présentées en se basant sur l'expérience acquise en agriculture. La production de triploïdes peut être considérée avec des manipulations chromosomiques, comme le transfert de segments de chromosomes et de gênes. De plus des transferts de chromosomes peuvent être envisagés ente espèces et lignées ne présentant pas d'interêt commercial mais qui apportent un caratère intéressant (ex : résistance à une maladie) absent dans l'espèce commerciale. La combinaison de la polyploïdisation et de l'hybridation augmente probablement les chances d'obtenir des clones parthénogénétiques de mollusques, non consanguins, présentant des gênes particuliers par rapport au type commercial. Les manipulations chromosomiques peuvent également être employées pour créer des lignes homozygotes utilisables pour des recherches intéressant d'autres mollusques, tels les embryons diploïdes provenant d'ovocytes tétraploïdes.

QUANTITATIVE GENETICS, OPPORTUNITIES FOR STRAIN IMPROVEMENT

A. MALLET *

RESUME. Les progrès récents de la recherche et du développement en aquiculture ont contribué à une meilleure compréhension des effets de la génétique et de l'environnement sur les caractères de production. Plus particulièrement, de nombreuses expériences avec différentes techniques génétiques justifient l'évaluation de leurs impacts probables sur les systèmes de production conchylicole. Il faut cependant considérer la grande diversité d'opérations en conchyliculture, variant des systèmes de production "clos" à ceux considérés "ouverts". Cette diversité influence fortement le degré possible de manipulations génétiques sur ces systèmes.

Les études électrophoretiques ont démontré une association positive entre la croissance ou la survie et le degré d'hétérozygosité chez les bivalves . Pour la croissance, le degré de cette association varie entre les stades du cycle vital, étant plus élevé au stade juvenile. Des gains importants en production sembleraient alors possible; cependant, des études récentes avec des animaux nés et élevés en captivité n'ont pu reproduire les résultats obtenus chez les populations naturelles. Cela suggère qu'une selection d'individus à partir de critères électrophoretiques serait peu efficace pour améliorer la performance.

Les études en génétique quantitative sur les bivalves sont relativement peu nombreuses. Elles ont cependant démontré une composante génétique importante pour la croissance et la survie. En plus, les expériences empiriques de selection artificielle ont pu changer la distribution phénotypique de certains caractères quantitatifs (croissance, résistance à la maladie) et une amélioration est prédite entre 20 à 30% par génération. La cytogénétique est discutée dans un autre chapitre (voir Longwell). Cependant, les données empiriques avec cette technique n'ont pu demontrer que de faibles gains. Comme conclusion, il semblerait qu'une approche de sélection à long terme serait désirable pour des systèmes clos. Si les juveniles sont capturés à partir de souches naturelles, alors l'identification et l'utilisation des souches naturelles supérieures par l'entremise d'une évaluation factorielle seraient à considérer.

ABSTRACT. Recent advances in aquaculture research and development have provided a better understanding of the environmental and genetical influences on production characters. In particular, numerous experimentations with different genetic techniques does justify an evaluation of their potential impact on shellfish production systems. Aquaculture consists of a wide range of practices, often classified into open and closed systems. This diversity needs to be considered since it will influence the extent of the genetic manipulation possible on these production systems.

From electrophoretic studies on marine bivalves, there is a consensus that growth rate is positively associated with enzyme heterozygosity. The strength of the correlation however varies with the developmental stages, being higher at the juvenile stage. Also, greater viability has been linked with higher heterozygosity

* Department of Fisheries and Oceans, Marine Ecology Laboratory, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth , N.S., Canada, B2Y 4A2

levels. On these grounds, one would expect some gains from isozyme selection. Recent studies on animals born and raised in captivity have failed to repeat the strong correlations observed in natural populations. This suggests that the electrophoretic screening of heterozygous animals would not provide substantial growth improvements.

Comparatively fewer quantitative genetic studies of production characters have been reported in marine bivalves. Most studies do report however an important genetic component for growth and survival. Artificial selection experiments have been very successful in shifting the phenotypic distribution of some quantitative characters (weight at 2 yrs, disease resistance) and gains of up to 20 to 30% per generation are predicted. Cytogenetics will be reviewed elsewhere (see Longwell, this volume). However, empirical results obtained so far suggest meager commercial improvement from this approach. In conclusion, it seems that a long term selection scheme for improving performance is the desirable approach for closed production systems. If seed supply is obtained from wild stocks, the assessment and utilization of this genetic resource available in stocks of diverse geographic origins should be analysed in a large factorial designs.

mots-cles : bivalves,genetique quantitative,electrophorese

keywords : bivalves, quantitative genetics, electrophoresis

INTRODUCTION

Compared to other cultured marine organisms the farming of shellfish species is characterized by simple husbandry and technology. Although a definite asset for exploitation, such simplicity may have limited the research and development of more efficient production approaches. Substantial reduction in production costs and improvement of product quality could however be achieved through the application of appropriate biological techniques.

This paper assesses whether the genetic improvement of shellfish species can be promoted and supported at the commercial level. This evaluation is influenced by several factors. First, aquacultural operations are diverse. They range from 'open' production systems which depend for the supply of juveniles on reproduction of species in their natural environments to 'closed' systems which depend on a self-contained nuclear stock propagated in hatcheries where recruitment is controlled by testing and selection. Such diversity imposes limitations on the integration of breeding schemes into production practices. Second, the scientific support from other disciplines is necessary. The effective development of any production system can only proceed in an integrated manner and on a broad front. Several disciplines, such as nutrition, disease prevention, technology, and ecosystem management will interact with genetics to influence production levels. Genetic improvement programs have a greater chance of success if all factors affecting both performance and costs are understood and integrated. Third, assessment of genetic potential depends ultimately on the soundness of the genetic information. From the animal and plant breeding literature we know that genetics has played a significant role in and accounts for approximately 30-40% of the total production improvement (Russell, 1974; Van Vleck, 1976). There is every reason to believe that at least similar levels of genetic improvement could be achieve in shellfish. However, comprehensive genetic studies are lacking in most shellfish and at present extrapolations are necessary from other better known breeding systems.

The potential commercial value of cytogenetics, electrophoresis, or quantitative genetics in aquaculture has received much attention. Cytogenetics will be discussed elsewhere in this volume (see Longwell). The genetic description of populations by means of biochemical techniques will be first examined, then quantitative genetics will be reviewed, and in the conclusion, their relative value will be evaluated for the enhancement of shellfish production.

1. ENZYME POLYMORPHISM

1.1. Technique

For the last two decades, the study of genetic variation in natural populations has been done primarily by gel electrophoresis. Mutations, the source of DNA variation, may provoke an amino acid substitution in a polypeptide. This may alter the net electrical charge as well as the three dimensional conformation of the polypeptide and such molecular variation can be detected by the separation

of stained proteins on a starch gel. The genetic interpretation of electrophoretic profiles is generally straightforward. For monomeric enzymes, homozygotes produce single stained bands whereas heterozygotes leave a two-banded pattern. For multinumeric enzymes, the banding patterns are more complex but the genetic extrapolation remains the same. Allele frequencies are determined directly from the electrophoretic phenotypes, expected frequencies of homozygotes and heterozygotes genotypes are determined using the Hardy-Weinberg equation, and these can be compared to observed frequencies.

1.2 Estimates of Genetic Variation :

There have been many descriptive studies of biochemical variation in marine molluscs over the past 2 decades. The extent of sampling varies tremendously among studies from a single population to several natural populations and from one or two enzyme systems to a large number of electrophoretic loci. These descriptive studies have established that many enzyme systems are genetically variable in a number of species (Littorina rudis, Ward and Warwich, 1980; Crassostrea sp., Buroker et al., 1979 a,b; Mytilus edulis, Ahmed et al., 1977; Patecla vulgata, Wilkins, 1976, 1977). In summary, (1) overall levels of polymorphism are high: one-third to one-half of the loci sampled are polymorphic; (2) average heterozygosity is generally high, 10-20%; (3) there are substantial differences in the frequencies of enzyme alleles among geographic populations (Gartner-Kepkay et al., 1980; Koehn et al., 1984); (4) spatial differences in allele frequencies tend to be correlated with certain environmental variables suggesting some form of selection (Koehn et al., 1980). Most of the evidence for a selection hypothesis (e.g., adaptation) is however circumstantial except perhaps for the LAP locus in Mytilus edulis (Koehn and collaborators).

What intrinsic value do these geographical surveys of electrophoretic variation have for the enhancement of production? Electrophoresis can provide inferences on the degree of reproductive isolation among genetic groups thus allowing mapping of the spatial differences in genetic composition (Koehn et al., 1984). This suggests that there are indeed genetic differences among populations of molluscs. However, such information has limitation in a breeding context since we cannot with ease evaluate the economic impact of differing allele frequencies among natural populations. It is the vegetative portion of the organisms, not the genes, that has commercial value. Electrophoretic surveys of genetic variation have served a useful purpose in the early 1970's in documentating the levels of genetic variability present in natural populations; however, the value of such surveys may be limited at this stage (see also Koehn, 1984) because of their lack of analytical and predictive power.

1.3. Connection between performance characters and biochemical markers :

The association between protein heterozygosity and production characters (growth rate, development stability, viability, morphological variance) appears to be a general phenomenon (although not universal) in many species (see Mitton and

Grant for a review, 1984). These associations have triggered a spur of optimism for using them in an applied context. The proposed approach would be one of electrophoretic screening of highly heterozygous individuals prior to the industrial growout.

1.3.1. Terrestrial Animals :

Much research in biochemical genetics of domestic animals has been stimulated by the hope of finding connections between biochemical and performance characters. If such connections were to be found and applied successfully, regardless of the reasons for them, the expensive task of evaluating animals and estimating heritabilities and genetic correlations would be circumvented. Neimann-Sorensen and Robertson (1961) and Smith (1967) have looked at the theoretical consequences of the use of genetic markers for improving performance. It was found that marker selection has more advantage if the heritability is low and if distant genetic relationships existed between tested animals. Empirically however, the postulated advantage of marker selection remains largely unsubstantiated. It was argued in many instances that when connections were established, they were mostly due to linkage or fortuitous gene combinations rather than pleiotrophy. For example, blood group being a property of the red blood cell was positively associated with milk production (Jamieson and Robertson, 1967). If the relationship between performance and biochemical traits is caused by linkage, the direction may change from population to population. For example, allele $B^{BO,Y,O}$ is connected with a decrease of milk fat percent in Scandinavian cattle breeds but with an increase within Holstein - Friesians (Pirchner, 1980). Also, if marker loci influence performance, either by pleiotrophy or linkage association, selected lines should differ in the frequency of such loci. Falconer (1973) investigated frequencies at 22 marker loci of selected mice lines and found only one line where differences were larger than that expected from drift. On the other hand, several experimental studies show that a wide variety of quantitative characters can in fact be found associated with specific genetic markers. In sheep, heterozygotes for isocitrate dehydrogenase were found to grow 10% faster than homozygotes (Baker and Manwell, 1977). A similar association between increased weight and heterozygosity levels was found in pigs (Rasmusen, 1981). Selection for increased yield in maize resulted in correlative allele frequency changes in three marker loci (Stuber et al.,1980).

Where marker selection may have the most impact in terrestrial production systems is when there is a direct connection between marker and performance effect. The close association between disease resistance in poultry and blood-group markers is not surprising since chemical structures on cell walls are intimately connected with virus to cell-wall interaction. Hence, Crittenden et al. (1970) showed a close connection between resistance to B group of leucosis virus and blood-group locus R. Cole (1968) was able to rapidly change resistance to Marek's disease by marker selection. Collins et al. (1977) reported mortality rates of the tumor infection in $B^{2}B^{1}$, $B^{2}B^{5}$, $B^{5}B^{5}$ genotypes of 5%, 26% and 93% respectively which would suggest a rapid improvement through the use of marker selection for disease resistance. Also, the value of new sources of genetic polymorphisms - restriction fragments length polymorphisms - has been consisdered

for plant and animal breeding (Soller and Beckmann, 1983). Basically, the overall quantitative value of a genetic marker is obtained from chromosome segments rather than single electrophoretic markers. Therefore, the probability of associations to quantitative characters is enhanced. The value of this approach is however greatly reduced for segregating populations due to associated decays of valuable linkages from recombination. This technique may prove to be valuable for selfing species with small genome sizes or for segregating populations in cases of low heritability.

With the exception of increased disease resistance and the determination of genetic relationships, the impact of marker selection has been negligible in terrestrial production system. The distant nature between the production characters of interest and what is actually measured (antigenic properties, enzyme polymorphism) appears to be the primary cause of failure.

1.3.2. Marine Molluscs :

Many empirical studies in molluscs have linked the level of protein heterozygosity with quantitative characters such as viability, growth rate, and physiological characters. Two marine bivalves in particular, Mytilus edulis and Crassostrea virginica, have been studied extensively and the subsequent discussion will focus primarily on that literature.

1.3.2.1. Viability :

Numerous electrophoretic studies of marine bivalve populations have revealed a deficiency of heterozygotes among juveniles (three-week old) and adult animals (see Zouros and Foltz, 1984 for a listing). The degree of the deficiency was found to vary with the age of the sampled animals (Zouros et al., 1983) being larger in the younger animals. The deficiency is also more likely to be expressed in certain enzyme loci (for example, LAP) than others. The mechanism controlling this phenomenon has been debated for several years. It has been attributed to a population phenomenon where animals in the sample would have originated from genetically differentiated populations (Koehn et al., 1976, 1984). An alternative hypothesis, assortative mating, predicts that certains genotypes have a greater likelihood of mating together than with other members of the populations (Foltz and Zouros, 1984). Recently, Mallet et al., (1985) have studied this deficiency in hatchery-produced juveniles and concluded that the origin of this deficiency is likely be in the larval phase and caused by a differential survival of the heterozygotes relative to the homozygotes. The data at this stage suggests that for viability at least, the association of heterozygosity and viability is very dynamic. Heterozygotes, as larvae, undergo a greater mortality but after metamorphosis, have a better survival than homozygotes.

1.2.2.2. Growth :

Associations of individual heterozygosity and growth rate have been documented in several bivalves species (see Gaffney and Scott, 1984). In a natural oyster population, Singh and Zouros (1978) and Zouros et al., (1980) observed a positive correlation between weight and heterozygosity levels. Similar results were reported for a natural mussel population where shell length increased with individual heterozygosity (Koehn and Gaffney, 1984). The generality of this phenomenon has been challenged however with several reports of failures to observe positive correlations in cultured populations (Wilkins, 1976; Beaumont et al., 1983; Gaffney and Scott, 1984; Adamkewicz et al., 1984). At least two explanations have been proposed to explain this discrepancy. First, these associations are thought to be highly dependent on the breeding structure of the population examined (Gaffney and Scott, 1984). Briefly, the effective number of contributing parents in laboratory crosses are thought to be insufficient to reproduce the positive association seen in natural populations. Rejection of this hypothesis would be brought about by the observation of a significant association in single crosses. Such positive associations in hatchery-produced juveniles have been observed in single crosses of the blue mussel, Mytilus edulis (Gartner-Kepkay et al., in preparation). Second, the discrepancy has been linked to a differing degree of environmental variation between laboratory and natural environments (Mitton and Grant, 1984). This could explain the failure to observe significant associations (although they were positive) in two of the three laboratory experiments (Gartner-Kepkay et al., in preparation). It was further proposed that the advantage of being heterozygotes should be accentuated under greater environmental heterogeneity but this will have to await further testing.

1.3.2.3. Physiological characters :

The advantages of being a heterozygote should be reflected in the underlying metabolic activities. Koehn and Shumway (1982) studied this relationship between heterozygosity levels and oxygen consumption in the American oyster. A negative correlation between oxygen consumption and heterozygosity levels was observed in both stressed and normally treated animals although under stress, the slope was steeper. This observation is consistent with the argument that more heterozygous individuals should have more energy to divert towards growth. Similar observations of negative correlations were reported in the clam Mulinia lateralis (Garton et al., 1984) and the snail Thais haemastoma (Garton, 1984). In addition, several reports have established a negative relationship between heterozygosity and morphological variability (e.g., lizards, Soule (1980); Mytilus edulis, Koehn and Gaffney, 1984); Fundulus heteroclitus, Mitton (1978)). This observation suggests a greater developmental stability in heterozygotes.

1.3. General Evaluation :

Many authors have argued that electrophoresis should play a major role in aquatic farming (Singh and Zouros, 1978; Singh and Zouros 1980; Ryman 1983; Foltz et al. 1983). This arguement is based on the premises that: (1)the resulting production gains in screening for more heterozygous individuals are

important, (2) these associations could be repeated in controlled production systems, (3) the relationship between individual heterozygosities and production characters is linear.

Although strong positive or negative correlations of individuals heterozygosity with production characters have been reported in natural populations, it should be realized that in these studies, individual heterozygosity was regressed against mean growth rate. The strength of the relationship is significantly weakened when individual performance is regressed against individual heterozygosity. For example in Crassostrea virginica, the R^2 is greater than 90% with mean weight but less than 4% when individual performance is considered (Zouros, personal communication). Also, estimates of variance components of heterozygosity classes for weight are less than 1% of the total phenotypic variance (Gartner-Kepkay et al., in prep., Adamkewicz et al., 1984 for an ANOVA)). This argues against large production gains through marker selection .

Gaffney and Scott (1984) concluded that the heterozygosity-growth relationship is of little value in a commercial operation. Their arguement is based on the disappearance of these correlations in cultured populations, a phenomenon they attributed to genetic structure differences between cultured and natural populations. There may be however other reasons. First, some of the discrepancies they observed can be attributed to the use of individual as opposed to mean performance in the calculation of the correlation. Second, correlations appear to be weaker in laboratory crosses although they can still be significant (Gartner-Kepkay et al., in prep.). The decrease in environmental variance in the laboratory environment may be a more likely explanation. Third, it is not still clear whether increased protein heterozygosity or lower homozygote performance accounts for the positive heterozygote-growth correlation. Homozygotes may have a poorer performance due to linked semi-lethal loci; hence, increased heterozygosity beyong the masking of these detrimental loci would not produce increased performance. The strength of the slope would therefore depend on how "bad" the homozygotes are. There remains also the question of the shape of the relationship with increased number of loci: will it be linear or will it taperred off and if it does, at how many loci?. It appears that numerous questions remain to be addressed before claims of an applied nature of electrophoresis can be made in bivalves.

2. Quantitative Genetics :

2.1. Technique :

Several approaches may be used to study the genetics of quantitative characters. It is sufficient to show that the distribution of phenotypes can be shifted or that progeny of extreme phenotypes also exhibit the parental characteristics assuming all other factors remain constant (i.e., environment). Whether this heritable tendency is dependent on nuclear genes, cytoplasmic genes, maternal components or a combination of these has to be demonstrated with more

rigid designs. The degree of heredity, the heritability (h^2), can be derived by measuring the resemblance of family members compared to unrelated individuals or by the slope of a parent-offspring regression. This parameter will assess the proportion of the total phenotypic variance that is genetically determined. Furthermore, since characters such as viability, growth and fecundity together determine the aggregate phenotype that will be used in a production system, it is necessary to know the direction and the magnitude of the genetic associations (pleiotrophy or linkage) governing these characters. Additive genetic correlation derived either from a selection design or a full-sib, half-sib design will estimate this relationship among characters. These two genetic parameters with the appropriate variance estimates for a number of economically important characters are the necessary tools for the establishment of a genetic improvement program based on quantitative theory.

2.2. Estimates of genetic variations :

2.2.1. Among Populations :

Most bivalve species are characterized by having many natural geographically-isolated populations reproducing under a wide range of environmental conditions. An accurate evaluation of average population performance and the characterization of the genetic resource are both necessary to insure all possible genetic gains in production (Turner and Young, 1969). Such evaluations are possible by means of analyzing pure population matings and their crosses when grown in common environments.

The importance of assessing the genetic resources prior to the initiation of a breeding program is well illustrated in the following example. The hatchery production of Ostrea edulis in Canada has been in operation since 1976 (Newkirk, pers. com.). The founding stock originated from an importation of O. edulis from Holland to the United States in 1948. Two stocks were established: (1) a hatchery-maintained broodstock at the Milford Laboratory, Long Island., and (2) a wild population established in Maine. Oysters obtained from Milford were subjected very successfully to two generations of selection based on weight at 2 years of age. In the first and second generation, a 23% and 16% improvement were recorded respectively. However, a recent comparison of the performance between the selected lines and unselected animals from the Maine wild population prove this latter to be superior not only in weight (they were 30% larger at 2 years) but also in many other respects (general hatchery performance).

To my knowledge, no extensive assessment of natural population performance for aquacultural purposes has been made anywhere in the world. We are currently assessing the performance of ten natural mussel populations in ten natural sites in Nova Scotia. This should provide the following information: (1) the extent of the genetic differences among populations for several commercially important characters (2) the ranking of sites for commercial production according to a biomass index; (3) the rigidity of the population classification across sites (testing for population interactions); and (4) the description of a population

response in different environments (whether the response is proportional or homeostatic). Most studies which have compared the performance of natural populations grown in common environments were done on a small scale and have little economic value. They have however shown that genetic differences exist between natural populations of a number of species for many characters. Also, that populations indigeneous to certain estuaries are not necessarily the fastest growing animals in these estuaries (Mallet and Haley, 1983b). For growth rate, Mallet and Haley (1983,1984) have observed genetic differences in larval, juvenile, and adult growth rate. Significant heterosis was observed for weight at market size and the choice of the right population for a given site would have produced a 25% increase. Similar findings were observed in Mytilus edulis through the reciprocal transfer of wild seeds among three sites (Dickie et al., 1984). For viability, it was found that stock was a primary factor in determining survival. In population crosses of the Atlantic oyster, lower larval survival and higher juvenile to adult viability were observed, a pattern that parallels what has been observed by electrophoresis. For disease resistance, geographically-separated stocks of C. virginica showed differential resistance to the parasite Haplosporidium nelsoni (Haskin et al., 1966). For physiological characters, Newkirk et al., (1977,1978) found a genetic basis to the variation seen in salinity tolerance within and between populations of C. virginica. Also, differential maturation rates have been noted on populations of C. virginica grown in a common environment (Loosanoff, 1969). There are certain problems inherent to most studies listed above. First, the number of contributing parents is generally small. Second, the number of sites and populations are small. Third, assessment of population performance from wild collection could be biased by any pre-collection selection. Also, estimates of performance from wild populations may nonetheless change with subsequent breeding under hatchery conditions. Mallet and Haley (unpublished) observed a change in the relative rankings of population performance after one generation in the hatchery.

2.2.2. Within Populations :

Population characterization and hybridization may provide improvement but they are only short-term techniques to achieve higher efficiency or to develop new genetic combinations for the development of useful varieties. Continuing long-term genetic improvement inevitably depends on multiple trait selection within stocks and is quantifiable as a percent annual improvement from the mean by using the following equation:

$$\Delta G/yr = i\, h^2\, C.V. / L \text{ (in years}$$

where i is the selection differential
h^2 - the heritability
C.V. - the coefficient of variation (the total phenotypic variation divided by the mean
L - the generation interval (in years)

This equation defines the selection gain for one trait and if selection can only be accomplished on one parent, we have to multiply 'i' by ½. The transmissible genetic effect, that is the heritability in the narrow sense, can be estimated by

numerous designs. However, unconfounded estimates can be computed only under certain breeding schemes and these parameters are very important since the transmitted genetic effects (h^2_N) can be offset by other genetic or non-genetic factors (i.e. maternal effects, non-additive genetic variance).

Several sib-analyses have reported relatively high heritability estimates for growth and survival (Lannan, 1972; Newkirk et al., 1977; Losee, 1979; Mallet et al., in prep.; Innes and Haley, 1977). It is remarkable at this stage that most estimates of heritabilities are based mostly on larval and early juvenile characters and on a small number of parents, that no estimates on characters at market size are available, and that these estimates are confounded by other genetic or non-genetic factors. In an attempt to provide unbiased estimators of these genetic parameters, Mallet et al. (in preparation) studied 30 half-sib groups of 3 replicated families each for larval growth and viability in the blue mussel, Mytilus edulis. In general, significant heritability estimates ranging between .16 and .60 for larval growth and .3 to .6 for larval viability were found. Positive genetic correlations existed within and between larval characters but there was a negative genetic correlation between larval viability and metamorphosis success. This trend may have been induced by a density-dependent effect and experiments are presently in progress to verify this hypothesis. Juvenile length at 6 months had a h^2=0.25 and a further number of heritabilities at market size will be computed. Based on these heritability estimates, we would expect the genetic gain to be in the range of 12% per year for growth.

Very few artificial selection experiments have been made to test this prediction. Artificial selection was successful in shifting the distribution of weight at 2 yrs of age in the European oyster, Ostrea edulis for 2 consecutive generations (Newkirk and Haley,1982,1983). The responses in these two generations were on the order of 23% and 16% respectively. Rapid changes in increased resistance to the parasite Haplosporidium nelsoni has been produced by mass selection (Haskin, 1979). These rapid responses agree well with the expected response in the first few generations of approximately 30% per generation due to the fixation of major genes (Wright, 1977). The mild inbreeding inherent in selected lines may enhanced the genetic improvement (Wright, 1977) presumably by accelerating the differentiation of traits favored under domestication. Also, simple propagation of wild stocks with no intentional selection in an artificial environment have induce substantial changes in the amphipod, Gammarus, (Doyle, 1983) and in the wild rice Oryza sativa (Oka and Morishima, 1970).

2.3. GENERAL EVALUATION :

The contribution of quantitative genetics to the commercial improvement of plant and animal species has been substantial and do not need to be reviewed here. In shellfish however, quantitative genetic studies have been virtually non-existent in comparison with the relatively abundant electrophoretic literature. Perhaps this is not surprising since most present production systems depend on the natural reproduction of the species for their supply of juveniles. Of those systems which have control over the reproduction, associated larval and juvenile rearing problems, either nutritional or disease related, assume most of the research

attention and as a result, unselected wild animals are used as founding broodstocks. It is possible that the added cost of running a breeding program is the limiting element: separate lines have to be maintained, animals have to be tagged and evaluated, and the breeding has to be rigidly controlled. However, we need to demonstrate that commercial production in shellfish species, as in their salmonid counterparts, can be significantly improved for greater economic gain through selection. There are a few small scale selection experiments which justify this latter claim; in oysters, reported selection experiments produced quite high responses for increased growth and disease resistance in a few generations (Beattie et al., 1980; Haskin et al., 1979;Newkirk, 1982,1983).

Heritabilities and genetic correlations for many economically important characters are necessary to properly assess the extent of potential genetic changes. Mass selection on single characters has been shown to work. It is possible however that negative correlated changes could be induced and impede the long term gain. For example, there could be important negative correlations between growth and reproductive performance (maturation, larval survival). A multi-trait selection approach based on a family index selection is probably the preferred route. There is however a need to investigate alternative improvement approaches. Inbreeding, which does not appear to cause drastic depression (Mallet and Haley, 1983), could be use in conjunction with crossbreeding for improved production.

For those production systems which depend on the natural reproduction of the species, some gains can be achieved through the evaluation of average population performance. We know that populations indigeneous to certain estuaries are not necessarily those that grow the fastest. The genetic ranking of these seed-producing populations obtained by growing them in common environments can provide enhanced production performance.

3. General Conclusions

The design of any genetic improvement programs is generally established from the following principles: (1) the assessment of the magnitude of the genetic variation, (2) the identification of the better gene combinations to be generated in the next generation, (3) the preservation of these genetic combinations through intermatings among individuals, and (4) the multiplication and release of superior varieties. Both step 3 and 4 would be common to quantitative genetics and electrophoresis insofar as specific genotypes need to be replicated; hence, similar costs would be generated. Therefore, it is for the assessment of the genetic variation and for the identification of the proper gene combinations (step 1 and 2) that the value of electrophoresis and quantitative genetics for improved shellfish performance has to be evaluated.

Many empirical studies have reported substantial discrepancies between estimates of genetic variation from quantitative genetics and electrophoresis (Turner, 1974; Jain et al., 1980; Kahler, 1980; Giles, 1984). For example, Giles (1984) found in 18 populations of the wild barley Hordeum murimum that the

electrophoretic variation among populations was virtually non-existent; however, the quantitative characters (i.e. seedling, developmental characters, morphological structure and flowering time) showed significant levels of heritable variability. The general inference in this case is that the divergence which has occurred on the quantitative characters has not been to the enzyme loci (Giles, 1984). Hence, inferences about the populations are very different whether based on biochemical or quantitative estimates. Although we cannot be sure, it is possible that selection for production characters works primarily on regulatory genes while electrophoresis evaluates enzymes which are products of structural genes. This for example could explain the observation of no electrophoretic differentiation between high and low selected lines.

The contribution of protein heterozygosity to the total variation in growth rate in shellfish has been misconstrued. The confusion most likely stems from strong correlations that are obtained in natural populations when mean performance within heterozygosity class is regressed against individual heterozygosity, a statistical manipulation that removes the within class variability. Indeed, when the percentage contribution of heterozygosity of the total variance in length is estimated, it is found to be less than one percent (Gartner-Kepkay, et. al., in prep.). Zouros (pers. com.) calculated that the R^2 of individual weight with heterozygosity is 4%, a decrease from 90% if mean weight is considered. These observations show that although positive associations are observed, heterozygous animals exhibit variable performance; therefore, the advantages of selection for highly heterozygous animals would be greatly diminished. Also, since the hypothesis of higher heterozygote mortality in the larval phase has not been rejected (Mallet et al., 1985), it is possible that screening and producing more heterozygous line would also produce lines with increasingly higher larval mortality. It would seem that the electrophoretic screening of heterozygous animals (Mitton and Grant, 1984) or the actual production of complementary electrophoretic lines to produce a highly heterozygous cross would not provide substantial improvement.

The improvement to the economic value of shellfish species necessarily depends on more than one character. The profit from an intensive oyster operation for example depends on survival, juvenile settlement, growth rate, meat yield and so on. This therefore suggest that selection should be applied simultaneously to several characters and not just one. Quantitative genetics offer several procedures in which where appropriate weights can be given to each component character, and where heritabilities, phenotypic and genetic correlations can be taken into consideration. The selection is then applied to a single index score and this approach yields the most rapid improvement of economic value (Falconer, 1981). For example, if negative correlations, for example between growth rate and larval survival, are found, then, there are methods to hold the genetic change in one character constant while increasing the other through the use of a restriction index. The possibilities of extension of the correlational approach to electrophoretic information is not clear.

It should be apparent from the foregoing discussion that any long term production gain will be dependent on a quantitative genetic approach. Where electrophoresis may have the greatest impact is in the selection of physiological characters. There appears to be a close association between aminopeptidase-I

polymorphism and hyperosmotic stress (Koehn and Immermann, 1981; Hilbish et al., 1982) which led to the establishment of sharp allele frequency cline between oceanic and estuarine environments. Presumably, if the economic gain was found to be important, a broodstock could first be standardized for a given allelic configuration prior to a selection program. The biochemical studies of resistance or susceptibility to common hatchery pathogens may also provide alternative improvement approaches to selection in shellfish lines as has been done in terrestrial production systems. Electrophoresis is also a key component of the infrastructure necessary for both efficient animal improvement and for better planning of experimental design. In a recent electrophoretic survey of 40 mussel families, 4% of individuals had wrong pedigrees (Mallet et al., 1985). Van Vleck (1970) has argued that mistaken pedigrees will not affect genetic progress as long as the fraction of false pedigrees is not large; for example, 20% error in progeny groups of 50 animals reduce the correlation for 0.88 to 0.82. In any case, the recognition that contamination was taking place enabled us to take preventive steps for its elimination. Another important contribution of electrophoresis is in pedigree control where the authenticity of a genetic relationship can be verified through electrophoresis.

Many of the empirical studies summarized here predict substantial production gains from the genetic improvement of shellfish. Based on these results, we should definitely promote and support the use of quntitative genetics in shellfish production systems, whenever possible. Perhaps the most serious limiting factor at this point is the lack of integration and sophistication of the industry. Juvenile supplies are highly dependent on the natural reproduction of the species and when hatcheries are used, they act as reinforcement in case of natural spatfall failure. The contrast with fish culture is overwhelming where fingerling production is almost totally controlled from hatcheries which encourage new development in other disciplines as well as initiating directional genetic changes. The rapid gain made by fish culture in recent years, especially in salmon and trout, should not come as a surprise and should be taken as a model by shellfish producers.

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DESCRIPTION OF CHROMOSOMES AND STANDARD CYTOGENETICS TECHNICS FOR WILD AND CULTURED SHELLFISH MOLLUSCS

A. LONGWELL *

RESUME : Comme la cytogénétique classique interface avec la biologie moléculaire et l'utilisation de la technologie de recombinaison de l'ADN, il y a un fort regain d'intérêt pour les études sur les chromosomes. Ceci a débouché sur des données nouvelles et stimulantes et une technologie nouvelle et puissante, résumée dans cette publication. Une telle méthodologie est certaine d'étendre, et peut-être même de supplanter l'utilisation des données courantes issues de la variabilité isozyme. Tout ceci va certainement modifier les idées sur la variabilité naturelle génétique et la façon dont les programmes de sélection sont menés, peut-être avec des avantages considérables pour la conchyliculture.

Les modifications des chromosomes sont importants dans l'évolution, et peuvent être essentielles pour le développement des lignées de coquillages plus adaptées à l'élevage commercial dans les conditions contrôlées des écloseries. On peut employer le génie chromosomique pour faire des triploïdes utilisables directement en conchyliculture. Les caractéristiques générales des polyploides sont présentées en se basant sur l'expérience en agriculture. En plus de la production des triploides, la manipulation chromosomique peut être employée pour transférer des segments chromosomiques de gènes ou des chromosomes entre espèces et lignées quand une souche ou espèce non commerciale porte une caractéristique souhaitable, par exemple une résistance aux maladies que ne possède pas la souche ou espèce commerciale. En combinant polyploidie et hybridation, les chances de développer, par parthénogèse de coquillages non consanguins, des clones de type génique commercial exceptionnel sont probablement optimales. On peut aussi employer le génie chromosomique pour développer des lignées génétiques homozygotes pour la recherche fondamentale et pour croiser les races, et pour d'autres coquillages intéressant la recherche, tels que des embryons diploides à partir d'ovocytes tétraploides.

Enfin, on donne l'exemple de la façon dont des individus mosaiques, même avec une lignée germinale en partie tetraploide, peuvent être employés pour initier une production commerciale des coquillages triploïdes. En même temps on peut employer de tels individus mosaïques pour entamer un programme de recherche qui puisse amener à la multiplication indéfinie des coquillages de génotype exceptionnel sans aucun croisement intersouche.

Une bibliographie importante est fournie avec une mise à jour des références ; elle contient des informations utiles sur l'état actuel de la cytogénétique et ses nouvelles méthodes, et le génie chromosomique.

ABSTRACT. As classic cytogenetics interfaces with molecular biology and use of recombinant DNA technology, there is a strong resurgence of interest in all aspects of chromosomes. This has resulted in exciting new information and powerful new technology summarized in this paper. Such methodology is bound to extend, and may even supplant use of much current data derived from isozyme variability. All of this is bound to influence views on natural genetic variability, and how selection programs are conducted, possibly with very considerable advantage to shellfish culture.

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* National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, **Milford**, Connecticut 06460, U.S.A.

Chromosome alterations are important in evolution, and may be essential to the development of shellfish strains more amenable to profitable culture under controlled hatchery conditions. Chromosome engineering can be used to make triploids of perhaps direct use in production of shellfish. The general nature of polyploids is reviewed, as is agriculture experience with them. Beyond production of triploids, chromosome manipulation can be used to transfer chromosome segments, genes or chromosomes between species and strains when a non-commercial form carries a desirable trait, as for disease resistance, absent in the commercial type. By combining polyploidy and hybridization, chances of developing parthenogenetic clones of non-inbred shellfish of outstanding commercial gene type are probably optimized. Chromosome engineering can also be used to develop genetically homozygous lines for basic research and for cross-breeding, and other shellfish of research interest, as diploid embryos from tetraploid oocytes.

Finally, an example is provided of how mosaic shellfish with even only a partially tetraploid germ line might be used to start commercial production of triploid shellfish. At the same time, such mosaics might be used to instigate a program of research that could lead to indefinite multiplication (cloning) of shellfish of outstanding genotype with no inbreeding at all.

A large bibliography is provided with up-to-date references containing useful information on the current state of cytogenetics and its latest methods, and chromosome engineering.

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mots-clés : bandes chromosomiques, in situ DNA hybridation, éléments mobiles génétiques, polyploidy, transfer de chromosomes, généagenèse, clone ...

key words : chromosome bands, in situ DNA hybridization, mobile genetic elements, polyploidy, chromosome transfer, parthenogenesis, clone ...

INTRODUCTION

Bringing new or different scientific technologies to bear in practical, profitable ways on previously unconsidered subjects must almost never be easy. Yet, the benefits which sometimes come about in unexpected ways often outweigh initial uncertainties, and have ramifications that could never have been anticipated. It must be recognition of this that led to inclusion of a consideration of cytogenetics at the Seminar on Shellfish Culture, Development and Management sponsored by the Working Group on Technology, Growth, Employment established at the '82 Versailles Summit.

Considering cytogenetics just now is particularly timely. In the last several years DNA research has provided new methods for chromosome study, and extended our information on them. New chromosome variability has been found which could change many concepts, some ways selective breeding programs and population genetic studies are conducted, and even ideas regarding genetic conservation of natural biological resources. The fascinating potentials recombinant DNA techniques promise for developing more productive plant, animal, and aquaculture breeds by transferring genes across absolute breeding barriers in single or multiple copies after cloning them in bacteria have been much discussed lately as in Kosuge T. et al. (1982), Chopra V.L. et al. (1983), Colwell R.R. (1983), and Arber W. et al. (1984). Yet, it is rather generally agreed, at least among major policy makers of U.S. agricultural research, that what we do not know about the structure and function of chromosomes in their role as gene regulators severely limits applications of recombinant DNA technology to improvement of food species, agricultural or natural resource (Committee on Biotechnology, Division of Agriculture 1983 and 1984). From the vantage point of fundamental science, organization of the eukaryotic genome into familiar chromosomes is one of the major, current problems in molecular biology. A 1981 report of the U.S. Office of Technology Assessment described the past impact of applied genetics on U.S. agriculture, and a 1982 report of the National Research Council discussed priorities in biotechnology research for international development (U.S. Congress 1981; National Research Council 1982). Neither, however, dealt with mariculture directly, and certainly not the current interest in using polyploids in mariculture. Chromosome engineering in its broadest contexts has yet to be much contemplated by mariculturists, let alone in relation to new DNA technologies.

In treating the very timely subjects of this paper, I freely use information on phenomena developed from study of a diversity of animals and also plants. This is not just because of the lack of much information on certain basic genetic aspects of marine resource or shellfish groups. At the cellular, chromosome and DNA levels there is underlying - but certainly not perfect - unity in so many basic phenomena, and techniques are mostly similar. Some phenomena are better grasped or studied in certain groups than in others. To limit the large number of references I refer to reviews of several recent and not-so-recent findings, and also to texts that should have long-term utility.

PART ONE

1. CHROMOSOME VARIABILITY AS SEEN AND MEASURED IN NATURAL AND ARTIFICIALLY BRED POPULATIONS

1.1. Basic View of Chromosomes and Variation Between and Within Populations at This Leve

Ordinary cytogenetic techniques provide information on chromosome number and position of the centromere, that is, the region of the chromosome associated with the

spindle apparatus responsible for orderly distribution of dividing chromosomes to daughter cells. Sometimes there are one or more non-centromeric, or secondary constrictions on the chromosomes. Distances from the centromeres to chromosome ends are measurable as is total chromosome length (Swanson C.P. 1957). See Figure 1. This kind of chromosome analysis can, to a large extent, be automated provided there is some additional expenditure for equipment (as, Graham J. and Taylor C.J. 1980). Cytogeneticists have not by any means fully exploited all existing potential in imagery (for example, the item in Chemical and Engineering News, page 22, January 21, 1985).

Observations of simple chromosome preparations with high-resolution light microscopy provide information on their spontaneous breakage and rearrangements which lead to duplication and deletion of their segments, their inversion within, or translocation within or between chromosomes. Such rearrangements sometimes lead to altered expression of genes or position-effects. Depending on the number, size and configurations of the species chromosomes, rearrangements are detectable with greatly differing levels of precision (Swanson C.P. 1957).

In wild populations of the well-studied fruitfly, Drosophila, frequencies of chromosomes with inverted segments vary in seasonal cycles, with drastic change in the course of a few years. Populations in the center of a geographic range have high levels of inversions, but these chromosome rearrangements occur seldom or not at all at the periphery (Wright S. 1968; Merrell D.M. 1981). Some non-aquatic groups, and possibly the lobster, have small accessory chromosomes which vary in frequency and distribution in natural populations suggesting they may have ecological significance (Roberts F.L. 1969; Jones R.N. and Rees H. 1982; Hughes J.B. 1982). In fish, notably salmonids, a common, well-known form of translocation is the dissociation of chromosomes in the centromere region to form 1-armed units and reassociation to form 2-armed chromosomes (Kirpichnikov V.S. 1981).

Chromosomes of economically important shellfish have not been much studied, and not often in much detail, and studies limited to few individuals. Early work seemed to indicate that, among shellfish then examined (Ahmed M. and Sparks A.K. 1970), oyster species at least had a rather conservative evolution at this level of organization (Longwell A. Crosby et al. 1967; Ahmed M. and Sparks A.K. 1967 and 1970; Menzel R.W. 1968). New, much needed attention to chromosome karyotypes of commercial shellfish is now determining some variation (Durán-González A. et al. 1984; Thiriot-Quiévreux C. and Ayraud N. 1982; Thiriot-Quiévreux C. 1984a, b). A useful list of recent cytological studies on bivalves is provided in Thiriot-Quiévreux C. (1984b). Arai K. et al. (1982) report on the chromosomes of the Pacific abalone.

Such information on chromosomes is the basis for examination of their intrapopulation variability, and for further structural and also molecular analysis of shellfish chromosomes at another level. As this variability is considered in toto, chromosome karyotype in shellfish breeding, restocking, ecology and genetic conservation takes on new meaning.

1.2. Variability in Banding Patterns of Chromosomes

Various staining procedures, the first described in 1968, produce patterns of bands on the chromosomes. These provide more sensitive data on chromosome variability than do arm ratios and length, and have rekindled interest in comparative chromosome cytology. Automated imagery of these patterns is also being developed.

A good review of techniques for banding chromosomes is Macgregor H.C. and Varley J.M. (1983), and on the mechanism of banding, Comings D.E. (1978).

The most generally important and useful bands are the C, G, R and NOR bands. The C banding often occurs in the centromere regions of the chromosomes. Heterochromatin is the densely stained chromatin long observed in chromosomes of some species after only simplest staining. The NOR bands are associated with important nucleolar-organizing regions of certain chromosomes.

Band patterns are inherited, and are mostly constant for a species. They have been described in great detail for various primate species which differ by chromosome rearrangements detectable at this level. There can be polymorphisms for bands within a species, as for the C bands of the human male sex chromosome. The NOR bands can also differ widely between individuals. Figure 2.

Since the introduction of C-banding techniques, it has become clear that the most common category of chromosome variation is number and size of heterochromatin segments. This may distinguish species, populations within species, and individuals within populations (Brutlag D.L. 1980). Variation in heterochromatin has been recognized in some fewer groups for many decades. Its variability has taken on heightened interest because heterochromatin is now known to contain highly repetitive DNA sequences supposed to have important functions in gene regulation. C bands are all generally taken to represent constitutive heterochromatin as opposed to the facultative heterochromatin of classic cytogenetics present in only certain cell types. Such general distinctions are no longer so easy to make, and may not have much significance in light of new procedures and information.

Chromosome banding techniques have yet to be applied much to resource or aquaculture species. There have been though some notable exceptions, particularly in salmonids (Yelenc J.G. 1979, Salvelinus; Rodríguez-Romero F. et al. 1979, American oyster; Uwa H. and Ojima Y. 1981, Oryzias). Use of band patterns in population genetic studies and in analyses of stock structure should be obvious. If heterochromatin indeed does regulate genes, there could be advantage to selectively breeding for C-banding patterns.

The low and erratic mitotic turnover of cells in marine resource and mariculture species may be as much a reason for the infrequent application of banding techniques to these groups as any. In the concluding page of his book, Genetic Bases of Fish Selection, V.S. Kirpichnikov (1981) lists development of a good, rapid chromosome technique for fish as one of three important goals for the future. This is not at all an unrealistic goal, and we might read fish to include shellfish.

Frequency of cells with chromosomes suitable for analysis in either fish or shellfish, the number and reliability of band patterns might be increased simply by fusing isolated cells or their nuclei to some convenient standard cell source with a reliably high mitotic frequency. Since the 60s, fusions of non-dividing with mitotic cells (Ringertz N.R. 1976) have been known to induce premature chromosome contraction of the non-mitotic nucleus (Rao P.N. 1982; Rao P.N. et al. 1982). Morphology of the chromosomes depends on the state of DNA replication of the nucleus. Some prematurely contracted chromosomes provide finer resolution of bands than do normal mitotic chromosomes. For example, there are 320 bands in the human chromosome complement at regular metaphase, but 1300-1400 bands in prophase-like, prematurely contracted chromosomes. Figure 3.

Successful fusions can be made between widely different animal groups. In some cases, premature chromosome contraction is induced even in fusions between plant and animal cells (Lima-de-Faria A. 1983). Fusion is achieved by treating cells with inactivated Sendai virus or with polyethylene glycol. Now an electro-cell-fusion apparatus is available (Zimmerman V. and Vienken J. 1982). Alternatively, shellfish nuclei might be exposed to the strong chromosome contracting factors (Gurdon J.B. 1968) abundantly present in early-stage frog eggs, or likely present in oocytes of shellfish and fish; or any available shellfish oocytes might be used to induce several sperm to develop their chromosomes in a single oocyte, as rodent oocytes are used for chromosome analyses of human sperm (Martin R.H. 1983). At least two antibiotics are generally recognized to relax chromosome coils, and might be helpful in producing more and better bands in the short oyster chromosomes. We have recently begun to explore the utility of such methods for shellfish and also salmonid cytogenetics.

1.3. Molecular Cytogenetics - a View of the Operational Chromosome

The proportion of singular, unique DNA sequences in various plant and animal chromosome complements varies from as low as 1-2% of all the DNA to half or more. Yet, most evidence indicates that it is these unique DNA sequences that contain most of the transcribed structural genes of the organism. The greatest portion of the DNA sequences in many eukaryotes consists of short, largely non-transcribed sequences repeated in long arrays (Setlow J.K. and Hollaender A. 1983). This is called satellite DNA because in density ultracentrifugation of isolated DNA it forms such a distinctly different band. Repetitive DNA sequences fall into 2 categories, moderately repetitive and highly repetitive, simple sequence DNA. These can be further subdivided into related families by density gradient ultracentrifugation and biochemical reassociation kinetics. Moderately repetitive sequences can comprise about 5-30% of all the DNA. For several reasons, repetitive DNA is believed to have a regulatory function in transcription of unique, single sequence DNA coding for proteins. As such, it could be the element on which selection operates when this is for quantitative or commercial performance traits.

A 1975 study reported on the DNA sequence organization of the American oyster, Crassostrea virginica, and the surf clam, Spisula solidissima, among 3 other marine invertebrates (Goldberg R.B. et al. 1975). All the genomes studied showed a major fraction of the unique sequence DNA to be interspersed with short repetitive sequences. Most of this DNA interspersed with coding unique sequence DNA is probably of the very short sequence type.

Total DNA content of the American oyster is near the low extreme in content for pelecypod mollusks, about one-half that of the surf clam, and only one-eighth that of the largest bivalve genome reported (Hinegardner R. 1974). The genome of the oyster was calculated to contain 4.7×10^8 nucleotide pairs. At least 60% of these are non-repetitive unique sequences.

Another study (Kamalay J.C. et al. 1976) provided additional information on DNA sequence repetition in the genome of the American oyster. This oyster at least has 2 classes of moderately repetitive DNA. Of these two, the longer is repeated on the average of 20 times when and where it occurs, and comprises 28% of all the C. virginica DNA. The other class represents 10% of the DNA. The latter contains sequences repeated about 3000 times. In addition, at least 1% of the oyster DNA of the repetitive class has related, but not identical sequences.

The spectrum of repetitive DNA in the American oyster is similar to that found n other mollusks. However, unique sequence DNA in the surf clam was found to be onger, more complex than in the oyster. In Spisula, less DNA fell into the longer sequence DNA lengths of the repetitive class. Also, Spisula has a shorter sequence class with more repeat copies. Further, reiteration of DNA sequences is higher in the gastropods (Collier J.R. 1971; Collier J.R. and Tucci J. 1980) than in bivalves.

This general pattern of DNA sequence organization of our familiar oysters and clams is similar to that in Xenopus (a toad), and different from that in Drosophila.

Two developments have made it possible to locate types of DNA sequences along chromosomes. One is the in situ hybridization method developed by Gall J. G. and Pardue M.L. (1971). The other is the molecular cloning technique for isolating and purifying DNA sequences. Once a particular DNA sequence has been multiplied by cloning in a suitable prokaryotic vector, it can be characterized in detail by restriction endonuclease analysis, or by complete nucleotide sequencing. Estimates can then be made of the copy number of the genes per chromosome set (Brandham P.E. and Bennett M.D. 1983).

The in situ hybridization technique consists of making the chromosome spreads on microscope slides, denaturing the DNA, and preparing a single-stranded complementary DNA or RNA probe. The probe is then allowed to hybridize onto recognition sites along lengths of the exposed chromosomes on the slides (Macgregor H.C. and Varley J.M. 1983).

This method can be used for quite precise localization of gene sequences. The technique could make selection for commercially desirable traits more efficient by detecting the presence of particular genomic DNA sequences or blocks of genes that determine character with savings in time, labor, and grow-out space (Flavell R.B. 1981; National Research Council 1982). (In the future monoclonal antibodies might similarly be used.) Figure 4. It has, perhaps more presently, obvious use in stock identification, and as a measure of genetic variability in natural populations. Such DNA diagnostic techniques are expected to be rather routinely used in breeding programs which will begin to have a dependency on them in the next 10 to 30 years.

Cloning of segments of DNA up to 40 Kb in suitable prokaryotes has become essentially routine in the last 5 years (Bennett M.D. et al. 1981; Dahl H.H. et al. 1981). We should begin cloning DNA segments of the oysters. Some of us at this conference might work cooperatively for a complete "library" of their cloned genes for in situ chromosome hybridization and other studies. At the University of California, Santa Barbara, D.E. Morse (1984) has recently started a collection of cloned DNA of the large, red, commercial abalone, Haliotis rufescens.

To date, best results have been obtained on in situ DNA chromosome hybridization techniques with the repetitive sequence DNA, and this class of DNA is easily isolated and purified. However, so many advances are being made in this area the state of the technology is bound to change rapidly. Until recently it has been necessary to use radioactively labelled probes and autoradiography to view the hybridization sites on the chromosomes. Now a technique has been developed in which probes are instead labelled with a biotin derivative of cytidine. Probes are detected on the chromosomes with an immunological technique, histochemical or antibody sandwiching method (Langer P.R. and Ward D.C. 1981). This procedure is easier to use, and it is just as sensitive as the radioactive label.

The in situ hybridization technique has already provided a fine resolution of repetitive DNA sequences along the chromosomes of some groups (Hamkaló B.A. and Papaconstantinov J. 1973; Brutlag D.L. 1980; Flavell R.B. 1981; Setlow J. K. and Hollaender A. 1983; Brandham P.E. and Bennett M.D. 1983). The nucleolus-organizing regions of the chromosomes have been found to be synonymous with the longer tandem arrays of repetitive DNA sequences. These regions contain the genes coding for 18 and 28 S ribosomal RNA associated with the nucleolus. (Ribosomes are essential for protein synthesis.) Ribosomal gene clusters in the bivalves were projected to represent less than 5% of the genome (Collier J.R. 1971; Kidder G. 1976a, b). These genes are more redundant in higher organisms. In groups where the ribosomal gene clusters are distributed over a number of chromosomes there is remarkable inter-individual variation in the location, site, size and number of clusters. This occurs even within strains and inbred lines (Bennett M.D. et al. 1981; Brandham P.E. and Bennett M.D. 1983). NOR bands of the chromosomes represent those ribosomal gene clusters which actively transcribed their message in the preceding cell cycle. There is a genomic control over transcription of these genes which has been much studied (McClintock B. 1934; Crosby, A. 1957; Longwell A. Crosby and Svihla G. 1960; Phillips R.L. 1978; Flavell R.B. and O'Dell M. 1979).

There seems to be a conservatism in the evolution of the nucleotide sequences of the ribosomal genes. Even ribosomal DNA from insects will hybridize with complementary ribosomal DNA from amphibians. This should enable us to use already cloned DNA of other mammals, Drosophila and sea urchins in initiating our studies on these nucleolar gene clusters in shellfish and in some salmonid studies.

Much of the more moderately repetitive DNA is clustered at the centromeres of the chromosomes or at their ends, but some is interspersed along the arm lengths. Its distribution corresponds to the C chromosome bands or heterochromatic chromosome segments. Moderately repetitive DNA is ubiquitous, but it is present in different forms, different lengths, different chromosome positions, and different amounts in various species and populations. This is just as are C bands.

In mammals, yeast and Drosophila most such dispersed, moderately repeated DNA sequences are movable genetic elements, or mobile genetic elements appear to be responsible for the transposition of these moderately repeated gene clusters from chromosome to chromosome within the cell (Pollard J.W. 1984; Shapiro J.A. 1983; Syvanen M. 1984).

2. MOBILE GENETIC ELEMENTS, CHROMOSOMES AND GENETIC VARIATION

Movable genetic elements were first recognized by Barbara McClintock more than 3 decades ago in maize through their genetic effects which were inconsistent with accepted models of mutation (see McClintock B. 1957). Apparent movement of these elements about the maize chromosomes affected the regulation and expression of a variety of genetic markers. Changes they induced were inherited. The mobile genetic elements of corn came to be recognized as similar to the transposable elements of prokaryotes. Such phenomena are known now to be quite common in eukaryotes (Shapiro J.A. 1983; Pollard J.W. 1984; Syvanen M. 1984).

Advantage has been taken of the large salivary gland chromosomes in Drosophila and of the in situ hybridization technique to study chromosome position of the dispersed, repetitive DNA that comprises mobile genetic elements. Its location was found to be highly variable between species and between stocks, and also between individuals, and to change in time over laboratory culture (Young M.W. 1979; Engels W.R. 1983). Figure 5.

As well as causing changes in gene regulation and expression, these motile elements can cause large-scale chromosome rearrangements of the sort already described here. The effects of these rearrangements range all the way from altered expression of single genes to subversion of the entire genome of the organism altering its overall genetic structure and information (Engels W.R. 1983). Importantly, these alterations often appear to be in physiological response to the organism's environment. Mobile elements are responsible for the chromosome rearrangements that accompany formation of active antibody-producing cells in mammals, and they are responsible for the switch in mating type in yeast. Many mobile elements though produce no clear phenotypic change. Their only effect seems to be to increase mutability.

At times, mobile genetic elements may be responsible for a majority of the observed mutation in a population, and they account for the high mutation frequency occurring in various populations from time to time. It is interesting to speculate here that the large numbers of fissions and fusions of the centromeres of fish chromosomes which provide polymorphisms even at the level of cells within individuals, and between individuals, and between populations may be under the influence of mobile genetic elements.

Motile elements are also involved in hybrid dysgenesis, the phenomenon of increased mutation, long observed in hybrid zones in nature, and in forced, artificially produced hybrid crosses. Hybrid dysgenesis is considered as having served an important role in the cultivation process of our crops and domestication of animals. Many of the mutations arising in various dysgenic hybrid crosses are unstable just as are those induced by known motile genetic elements. We can only wonder what role mobile genetic elements might play in development of shellfish culture, what role they have always played in resource populations of shellfish, and if we here are to learn anything about their function in our molluscan resources.

The vast array of quasi-stable genetic elements now known to occur widely is difficult to incorporate into the traditional view of evolution as slow accumulation of genetic change and speciation over long times. By disrupting gene regulatory systems, these elements seem capable of effecting change over shorter periods than ever anticipated. This could provide a mechanism for speciation, and account for the rapid genetic changes which must have occurred in domestication of animals.

Particular significances of mobile elements for quantitative genetics, population genetics, traditional plant, animal, aquaculture breeding and domestication of aquaculture species have barely begun to be considered, or not considered at all as yet. The powerful effect of selective breeding probably does not produce progress so much by recombination and selection of structural genes as by recombination and selection of gene regulatory sequences of the chromosomes. If so, selective breeding might be more efficiently, directly, practically practiced in the future on regulatory sequences than on particular production traits. Regulatory genes, the mobile elements, might be practically modified using recombinant and other DNA techniques. Clearly, however, for now there are mobile genetic elements that can and do alter gene regulatory systems. It is ignorance of gene regulatory systems that limits utility of gene transfers recombinant DNA technology makes possible. For such reasons, competitive grants in molecular biology available from the U.S. Department of Agriculture for work on plant, animal or aquaculture species of food value are being prioritized on the basis - not of promise of immediate practical applications which will always have restricted use - but rather on the basis of how much might be learned of genome structure and function of the particular commercial species (Committee on Biotechnology, Division of Agriculture 1983 and 1984).

Because moderately repetitive DNA and the C chromosome bands have been linked to mobile genetic elements, their potential for instability should be kept in mind in using nucleotide sequences, size, and chromosome position of these gene clusters or chromosome bands in any such population studies of shellfish we might hope to see in the future. Because these non-coding gene clusters further may be implicated in cell differentiation, it seems wise and interesting to compare patterns from different tissue sources.

P A R T T W O

1. CHROMOSOME ENGINEERING

What must be intricately programmed, structural rearrangements of chromosomes under the influence of mobile genetic elements, as in antibody-producing cells, suggests that someday specific induced changes at this level may be possible. For now, however, chromosome engineering concerns mostly manipulation of whole chromosome sets as the induction of triploidy for hatchery culture of fish and shellfish. Largely because of the pioneering work of wheat geneticist Ernest R. Sears, chromosome engineering in cereal crops entails more - development of chromosome addition, and chromosome substitution lines, and translocation of chromosome segments between lines - all transferring useful genetic material from one to another species or variety. Lately interest in transfer of genes via recombinant DNA techniques has led to suggestions that the transfer of microscopic-level chromosome fragments, as perhaps cloned in tissue culture cells, could be a more immediate direct approach in some breeding programs (as Pirrotta V. et al. 1983; McBride O.W. and Peterson J. L. 1980).

2. BACKGROUND

2.1. Spontaneous Changes in Chromosome Number

Polyploidization, the increase in chromosome number by a full set of chromosomes, is involved in speciation (Beatty R.A. 1957; Stebbins G.L. 1970; Lewis W.H. 1980). Elegant studies by Sears in the U.S. and independently by Kihara in Japan largely repeated this process for bread wheat (see Sears E.R. 1959). Polyploidy remains the best understood of all mechanisms contributing to speciation. In this regard, considered use of artificial polyploids of marine species in nature adds a new dimension to efforts at curbing introduction and transfer of exotic species by creating new types with native germ plasm.

Many of our most important crops are tetraploids with known wild relatives that are scrawnier but tougher - wheat, cotton, tobacco, potatoes. Tulips are tetraploid. Mammalian liver cells are polyploid. Polyploidy seems to have occurred several times in the evolution of fishes. As so generally known, salmon have a tetraploid ancestry (Kirpichnikov V.S. 1981).

Nearly all natural polyploidy in higher plants occurred in plants of hybrid origin (allopolyploidy). By contrast, much of the polyploidy in animals is autopolyploidy, duplication of the same species set of chromosomes.

Individual plants and animals also occur with more or less than an exact multiple of the entire basic chromosome set, a condition limited (outside of tissue cultures and tumor cells) to one or two chromosomes at a time (aneuploidy). Plants

or animals which have already undergone polyploidization are more tolerant of aneuploidy than others. Due to the work of Sears E.R. (1954), bread wheat has an extensive series of aneuploid lines, more complete than for any other species of plant or animal. Trisomic fish with an extra chromosome are occasionally found in groups that have undergone polyploidization. Natural salmonid populations are reported with varying numbers of chromosome arms (Kirpichnikov V.S. 1981). Aneuploidy in humans is commonly known to have severe untoward effects, and is usually lethal except for the smallest and sex chromosomes.

Of all the wild American oysters examined in my laboratory in the course of different studies, we have never come across an aneuploid or polyploid specimen. However, aneuploid, polyploid and haploid cells are common in early cleavage embryos (Longwell A. Crosby and Stiles S.S. 1968; Stiles S.S. and Longwell A. Crosby 1973), a phenomenon also observed by Menzel R.W. (1968). In examination of over 1600 eggs from 17 mass-spawned groups of 835 wild Crassostrea virginica, a mean 12% were heteroploids of one type or another. More specifically, 6% of the embryos were haploid; 15% were polyploid; 1.5% hypodiploid; 1.5% hyperdiploid; and another 1.5% chromosome mosaic (Stiles S.S. and Crosby Longwell A. 1973). However, it is worth noting that these frequencies vary widely from spawning to spawning. Heteroploid embryos must have poor chances of surviving in regular larval cultures. Only infrequently is an aneuploid or tetraploid oocyte ever observed among spawned oocytes of any female. Possibly some of the very undersized spat that occur in most cultures of American oysters were at least primary haploids as embryos.

In nature, plant polyploids occupy a different habitat from their diploid relatives. This suggests they have a different tolerance or wider range of tolerance to unfavorable environmental conditions than do the diploids. This though must depend on the characteristics of plants initially hybridizing. Polyploid plants are not successful in competing with diploid parents in the same niche. In North America certain polyploids of Tradescantia (the spiderwort) grow rampant under an unusually wide range of ecological conditions. As well as providing a background of information to consider in induced polyploidy, such facts are worthy of note as prospects for stocking artificial polyploids of resource species in nature, as for use in salmon ranching, begin to be practically entertained for salmon after having been first remarked on in respect to shellfish about 20 years ago (Longwell A. Crosby 1968; Utter F.M. et al. 1983).

2.2. General Nature of Polyploids of Interest in Relation to Their Use in Mariculture

Two universal characteristics of polyploids are 1) their increased cell and nuclear size, and 2) their reduced reproductive potential (Beatty R.A. 1957; Swarup H. 1959; Stebbins G.L. 1970; Lewis W.H. 1980).

In plants, gigantism is often but certainly not always associated with polyploidy. Although cells are larger, there are simply fewer of them, and some evidence they divide more slowly. Certain organs may be disproportionately increased in size, and have somewhat different shape or texture. This latter could be as important for some shellfish culture as any enhanced growth. Growth rate and physiological development of polyploids are often slower than in their diploid counterparts. The effects of increasing levels of polyploidy are not progressive, and very high degrees of ploidy lead to dwarfism.

The poor seed set of polyploid plants has one cause in the abnormal segregation of chromosomes in meiosis due to their faulty pairing in meiotic prophase. In both

fish and shellfish considerable gonad is developed prior to chromosome pairing in maturing oocytes. This chromosome phenomenon then alone cannot be expected to conserve as much energy for somatic growth as would absolute sterilization. Oocytes with only improperly paired chromosomes should go on to develop rather mature but useless gametes that produce largely lethal zygotes. However, if these are not spawned, at least in shellfish as the American oyster, their resorption could increase energy for somatic growth.

It seems though that chromosome non-disjunction is not the only basis for infertility in polyploids. Imbalances in gene regulation due to increases in gene number appear to be responsible as well. Studies in maize, lettuce and the snapdragon flower point clearly to this.

Expression of genes generally is modified in the polyploid relative to diploid state. Polyploids, in fact, provide molecular models for research on gene regulation of the sort basic to any exploitation of present-day potential of inserting multiple copies of genes cloned in bacteria back into their original host or into new ones. Specific studies on gene regulation in polyploids have concentrated on the more directly studied ribosomal gene clusters at the NOR chromosome bands. Ribosomal gene number in polyploid bread wheat has not been reduced in evolution from the sum of the ribosomal number of parent grasses. Instead, synthetic activity of these genes is regulated at the transcription level (Crosby A.R. 1957; Longwell A. Crosby and Svihla G. 1960; Flavell R.B. 1981). In diploid hybrids, as well as in allopolyploids, there is differential transcription of the ribosomal genes derived from different ancestor species. Recently fishes were found to have a polymorphism of the NOR chromosome bands (Foresti F. et al. 1981). Although salmonids are descended from a recent tetraploid ancestor, they too have regulated expression of extra copies of unreduced numbers of ribosomal genes (see Lima-de-Faria A. 1983). There is the possibility newly induced polyploids would not so efficiently limit expression of genes as do old, naturally occurring polyploid species.

How certain modified behavior of ribosomal genes in polyploids affects production characters is unknown. There is no model as for heritability of quantitative traits for predicting how polyploidy will affect expression of genes designating commercial traits to shellfish. This will be known only from inducing, hatchery- and field-testir the particular polyploids in question.

Both plant and animal haploids and polyploids have a well-documented tendency to revert to the diploid number of chromosomes by adjusting critical mitotic divisions. Aneuploid chromosome sets tend to do the same, and unpaired meiotic chromosomes also tend to misdivide at the centromere. Seeming haploid and polyploid adults then could be either somatically stable or unstable mosaics. Polyploidization is known to be associated with some tissue and cell differentiation, and it cannot be excluded that somatic reduction of the chromosome number also plays some role. Some tissues are likely to tolerate better or less well artificial ploidy levels, and be more or less likely able to revert to being diploids. This could account for the well-known fact that polyploids at least in plants often have disproportionate organ sizes. This should be considered when appraising the success of induced polyploidy.

After about 40 years of experience with induced polyploidy in plants, agriculturists now know that it is no panacea for plant improvements. Not every species hybrid is converted by polyploidy into a vigorous, fertile form, and some can be eliminated as unfit immediately. Fewer induced polyploids are cultivated now than some years ago. Still polyploidy is acknowledged as one of the most promising means

of increasing yield in some plants. Induced autopolyploidy is regarded as having great potential in perennial forage grass. The most publicized polyploid, triticale, an allopolyploid of a wheat-rye hybrid, is better adapted to marginal lands than is wheat, and has the good protein quality of rye.

The fact that years of plant studies on polyploidy point as major developments to a synthetic polyploid for use in marginal land, and as a wild crop ought not be lost on mariculturists contemplating stock enhancement programs. A particularly interesting development in this regard would be use of polyploid hybrids which could have the advantage that polyploidy made their hybrid state true-breeding, permanent. This was remarked on by Chevassus B. (1983) in his review of inter-species hybridization in finfish, and by Longwell A. Crosby (1968) for shellfish.

Aside from aquaculture, research on polyploidy in animals in recent years has been of a very basic nature and on experimental species. Performance of salmon with induced triploidy is beginning to be measured (Lincoln R.F. and Hardiman P.A. 1982; Purdom C.E. 1983; Wolters W.R. et al. 1982). That of triploid shellfish is also being studied (Allen S.K. Jr. et al. 1982, soft-shell clam; Stanley J.G. et al. 1981, 1984, American oyster; Tabarini C.L. 1984, bay scallop, Argopecten irradians). Because polyploids generally perform differently in pure and mixed stocks, shellfish triploids need to be performance tested together with their diploids, and apart from them. Because the benefits both salmon and shellfish culturists look for from polyploids are so strongly mediated by sexual development - better meat quality during reproductive season, more energy for somatic growth, less seasonal mortality, sterile animals for management - influences of the extra chromosomes on reproduction have to be carefully documented. Also, of course, performance tests must be conducted throughout the life cycle at least to the expected age of sexual maturation. Unless polyploidy confers some overall advantage other than that associated with proved reduction in gametogenesis, any commercial production of triploids will have to compete in the future with any alternate method of sterilization that does not confer any further disadvantage than polyploidy.

Just as in any other kind of breeding program, the character of the polyploid will be affected by the parental stock. Polyploids with parents of different species might have fewer detrimental effects and ought to be considered seriously.

3. CHROMOSOME ENGINEERING AS PRESENTLY PRACTICED IN A BROADER CONTEXT

For several reasons it would be a mistake for mariculturists to limit their interest in cytogenetics and polyploidy at this time to only inexpensive production of such that outperform parental diploids.

The performance of a newly induced polyploid plant that determines its immediate economic success or failure becomes relatively unimportant when the polyploid is used only as a means of facilitating gene transfer between chromosomes or species. This is accomplished by restoring fertility through polyploidization of the hybrid. The fertile polyploid is then backcrossed to the more generally adapted parent. Progeny are selected for the trait to be transferred from the less generally suitable parent. Selected F_2 progeny are again backcrossed to the better adapted parent, offspring selected and backcrossed again. This is continued until a strain is developed which combines all the original traits of the one parent with the introgressed gene of the other, or has all the chromosomes of the one parent except the substituted one of the other bearing the desired gene. Plant breeders most frequently use this

means to transfer simply inherited traits, as for disease resistance, but complex characters have been transferred in this way as well.

In terms of general applications, it seems agreed that polyploidy has at least one of its greatest and most varied uses in plant breeding as such a means of genetic transfer in more sophisticated forms of chromosome engineering (as Lewis W.H. 1980). Transfer of disease resistance from wild species to cultivated varieties via induced polyploidy has become a relative standard practice in the breeding of many crops - wheat, oats, cotton, tobacco. So little is known about the nature of disease resistance in shellfish, it is difficult to surmise how useful this technique would be in that regard, but that is only one use of the breeding procedure.

In cultivated wheat particularly, there has been a long history of this sort and related chromosome manipulations. Much of this was made possible and stimulated by the development of the extensive and complete series of aneuploid wheat strains (Sears E.R. 1954). This series includes for each of the twenty-one chromosomes of hexaploid wheat with its basic set of 7 from 3 different ancestors: a series of monosomic strains missing one member of the chromosome pair; trisomic strains with one extra chromosome; tetrasomic strains with 2 extra chromosomes; strains missing one chromosome arm and with the other present as a telocentric chromosome or isochromosome; nullisomic strains in which one chromosome pair is entirely absent; nullisomic-tetrasomic strains where the absence of one chromosome pair is compensated by the presence of an extra pair of the corresponding chromosomes from another of wheat's three ancestral species. These lines have enabled the cytogenetic analysis of wheat to be conducted with an elegance unsurpassed in any other organism.

As far as we know, commercial shellfish are not normally polyploid, so it is highly unlikely an aneuploid series of strains could be developed in any of them as they are. However, if polyploid strains were first developed, at least partially complete aneuploid strains could well be possible. It is worthwhile then to reflect on chromosome engineering as it might be done with aneuploid lines using the methods and outcome of wheat breeding experience as an example.

Aneuploid strains as available in wheat facilitate the transfer of single chromosomes between cross-compatible groups (Lewis W.H. 1980; Chopra V.L. et al. 1983). Addition lines can be bred with an extra chromosome - for any one of the complement, or any partially homologous chromosome of one parent type exchanged for the corresponding chromosome of another of the polyploid parent species (substitution lines). Although these possibilities cannot be entirely excluded for diploid stock, natural or induced polyploid stocks make chances of success much greater.

Various chromosome addition lines have been produced in wheat which contain a single chromosome of rye, barley, and wild grass species. Intervarietal chromosome substitution lines tend to be stable. However, those in which chromosome substitution has been between more widely varying groups tend to be unstable cytologically reverting back to one parental type. Figure 6. Substitution lines tend to be more stable than addition lines, and some have been directly used in commerce. Figures 7 and 8.

Overall performance of substitution lines still tends to be depressed in spite of their improvement for some specific character. Sears demonstrated that radiation could be used effectively to transfer segments of chromosomes, as opposed to whole chromosomes, between cross-compatible groups. This is accomplished through induced breakage and recombination of broken chromosomes. Using this procedure, a piece of

chromosome from a wild grass relative bearing disease resistance was transferred to wheat (Sears E.R. 1959). By now, fourteen such transfers of disease resistance have been bred into productive cultivors of tomatoes, and other specific transfers have been made in wheat, potatoes, barley and tobacco. Figure 9.

An induced chromosome deletion in wheat (Sears E.R. 1976) provides another means of gene transfer by promoting pairing of the partly homologous chromosomes from different hybrid parents. The natural crossing-over between genes on paired chromosomes in the presence of this deletion occurs with a frequency allowing the practical transfer of the desired gene onto the chromosome of the better performing parent.

Use of recombinant DNA probes, restriction endonuclease analysis, in situ hybridization, and chromosome banding should all enable the direct monitoring of chromosome transfer techniques just as they enable the detection of cloned DNA sequences.

Experience of plant breeders with transfer of whole chromosomes, chromosome arms, chromosome fragments, and chromosome-mediated gene transfer provides a practical basis for serious consideration of prospects for gene transfer using recombinant DNA techniques. The opinion has been expressed that recombinant DNA techniques will be useful to transfer genes across absolute breeding barriers, but when such breeding barriers do not exist, chromosome transfer techniques will continue to be used. One of the attractions of direct DNA transfer is that it can - like polyploidy - theoretically be achieved without generations of crosses. However, it has other limitations - need to identify genes, develop means for their mass transfer, the need for these to be stably integrated into the chromosomes of their new host.

Another aspect of chromosome engineering appropriate to either doubled or diploid inter-species hybrids of shellfish would be use of intermediate hybrids as bridges between two otherwise incompatible species (Longwell A. Crosby 1976; Ueda et al. 1984). This could be for the purpose of transferring disease resistance, or simply for making more complex mixtures of the traits of two species otherwise impossible to cross. As in plants, there would have to be backcrossing to the better adapted, more standard commercial form with selection. Inter-species hybridization has not been so studied in commercial mollusks as in fish, leading to wonder why shellfish biologists have had little interest in such hybrids and fishery biologists so much. Menzel R.W. (1968) did report on several Crassostrea species hybrids. Stenzel H.B. (1971) and Ahmed M. (1973 and 1975) describe the fascinating wealth of oyster species. In most, but not all Menzel's crosses hybridization was easily achieved. Unfortunately, one of the most interesting hybrids, that of the American and Japanese oyster (C. gigas), invariably dies at an early age as first shown by H.C. Davis (1950) of the Milford Laboratory and more recently confirmed by S. Stiles (1978). Some work has begun on achieving a polyploid hybrid. Except for limited quarantine space for exotic species we would be using bridging species crosses as well.

4. SIGNIFICANCE TO MARICULTURISTS OF THE ASSOCIATION IN NATURE OF HYBRIDIZATION, POLYPLOIDY AND PARTHENOGENESIS

In both the plant and animal kingdom, the vast majority of apomictic species which have replaced sexual reproduction with various types of asexual reproduction are polyploids with a hybrid origin. Yet, the exact relationship between apomixis, polyploidy and hybridization is not clear - whether parthenogenesis is promoted in

these types, or whether it is a chance occurrence which simply allowed their survival in evolution (see Swanson C.P. 1957). The most common form of polyploid production in nature is through the occasional failure of meiosis with a resultant diploid egg which, when fertilized by a haploid sperm, results in a triploid. In turn, oocytes from cytologically unstable triploid females often fail to undergo meiosis. Such eggs with 3 chromosome sets yield tetraploid progeny with 4 chromosome sets when fertilized.

An aquatic example of spontaneous apomixis in invertebrates is the brine shrimp which have a number of polyploid strains with 3, 4, 5, 8 and 10 sets of chromosomes, all parthenogenetic races of only females. Apomixis also occurs in nature in teleost fishes where it is again associated with hybridization and polyploidy. Several species are reproduced almost exclusively by gynogenesis or hybridogenesis, and are almost exclusively female. Gynogenetic forms require fertilization, but the chromosome material of the sperm is inactivated in the ooplasm. Reduction division of the oocyte chromosomes is inhibited (see Cherfas N.B. in Kirpichnikov V.S. 1981). This phenomenon also occurs in amphibians.

Natural parthenogenesis also occurs where the second meiotic division, not the first, is inhibited; or the female pronucleus fuses with the second polar body, or where haploid development commences and the diploid chromosome number is restored at cleavage mitosis. In the latter case, progeny will be almost totally homozygous. When such a form of gynogenesis is induced anew in oocytes of females bred this way, the result is clones of highly inbred individuals genetically identical to the sole parent.

Different forms of parthenogenesis could have much utility in shellfish culture, and in needed fundamental genetic study of shellfish species. The obvious basic uses are of heterozygous clones of non-inbred superior parents, and homozygous clones or pure lines for cross-breeding. Should direct DNA transfer of genes or direct chromosome transfer be effected, parthenogenetic techniques will be important in multiplying those few individuals with successful transfers. This would also be the case for more traditional chromosome transfer techniques in any non-inbreeding species as are seemingly all commercial shellfish, and just about all mariculture species.

However, development of parthenogenetic lines of shellfish will probably entail a serious commitment. Gynogenesis has been induced in several fish groups, but the frequency with which this is successfully done varies greatly. Large stocks of gynogenetic fish seem to have been obtained only in the carps (see Cherfas N.B. in Kirpichnikov V.S. 1981). The recent success of Streisinger G. et al. (1981) in establishing pure lines of the zebra fish, Brachydanio, may be attributed to his use of already inbred lines purged of lethal genes by many generations of traditional close relative matings. Still, in view of the low cost of maintaining oysters compared to salmonids, the establishment of gynogenetic strains seems inexpensive. Such efforts ought to be promoted. Arai K. et al. (1984) reported on the induction of gynogenesis in Pacific abalone using ultraviolet-treated sperm (also Arai K. et al. 1983; Naito et al. in press).

Shellfish eggs at spawning can be manipulated at either the first or second meiotic division, unlike fish which are at spawning beyond manipulation of meiosis I (Longwell A. Crosby and Stiles S.S. 1968). Even though perhaps mostly abortive, oyster eggs, as already noted, not infrequently begin parthenogenetic development (Stiles S.S. 1973; Stiles S.S. and Longwell A. Crosby 1973; Longwell A. Crosby and Stiles S.S. 1973).

The entire process of fertilization, resumption of meiosis and cleavage, obscure in finfish, can be followed in the shellfish oocytes and cleavage in great detail. This, combined with the opportunity of introducing minute chromosome fragments through less than totally inactivated stimulating sperm, suggests the possibility of obtaining in this manner fundamental information on subchromosome transfer espoused by some as an alternate to transfer of cloned genes. The transfer of such fragments in fish was clearly demonstrated recently by Chourrout D. (1983), and in shellfish by Stiles S. (1978) and Stiles S. et al. (1983).

Almost since the beginning of marine biology, molluscan eggs have been used extensively for many aspects of cell and developmental biology, and now they are being used for molecular studies (Morris M. 1917; Raven C.P. 1961 and 1966; Longo F.J. 1972 and 1983; Verdonk N.H. et al. 1983). This provides a great wealth of helpful background information.

Mutants that alter the behavior of meiotic chromosomes in ways useful in establishing gynogenetic and parthenogenetic strains are known to occur sporadically in several groups of invertebrates (Baker B.S. et al. 1976; Yamaguchi M. and Lucas J.S. 1984). These might be found as well in commercial shellfish. Selection for natural occurrence of parthenogenesis has been successful in Drosophila (as Carson H.L. 1967).

A first effort was made to induce gynogenetic development in the American oyster (Stiles S. 1978). Because of the inconvenience of traveling some distance to use an X-ray machine and belief that ultraviolet treatment of sperm would give more clear-cut results, new work is presently underway using UV. Stiles S. et al. (1983) briefly discussed prospects for successfully inducing different forms of parthenogenesis in the oyster on the basis of cytological appraisal of eggs subjected to high pressure treatment and to ultraviolet.

Because commercial shellfish have no known polyploidy in their evolution, induction of haploid parthenogenesis or even that resulting from fusion of the female gamete with the second polar body ought best be attempted with oocytes of fertile tetraploids. Further, the genetic variability and instability generated by hybridization and polyploidy, particularly in regulation of ribosomal gene clusters implicated in chromosome pairing (Young M.W. 1979), indicate obvious benefits of polyploids and hybrids for inducing parthenogenetic development of the type not entailing any true meiotic division at all.

5. DEVELOPING TETRAPLOID SHELLFISH TO PRODUCE TRIPLOIDS BY REGULAR BREEDING

Induced tetraploidy is not so well-tolerated as triploidy. Even so, because more regular chromosome pairing can occur in meiosis, viable gametes with complete chromosome sets can be formed, and lines can be maintained by normal mating.

"Somatic" doubling of the germ line may be as feasible a means of producing tetraploid shellfish as any, excluding cell fusion techniques, and a more efficient way of inducing triploidy than by suppression of the second meiotic division (Longwell A. Crosby 1968; Longwell A. Crosby 1983). This has precedence in plants where polyploidy is often induced at somatic growing tips that are to produce a new flowering shoot. It is a different procedure from that practiced now quite a bit on amphibians, fish and shellfish eggs (as already cited; Nagy A. and Csanyi V. 1978; Gillespie L.L. and Armstrong J.B. 1979; Reinschmidt D.S. et al. 1979; Farinella-Ferruzza N. and Vitturi R. 1981; Yamazaki F. 1983; John G. et al. 1984).

Almost any sample of fertilized oyster eggs shows them to be in asynchronous stages of meiosis, fertilization and cleavage. For this reason, prospects of routinely producing large numbers of polyploids through experimental treatment of shellfish eggs in hatcheries may be limited. Sorting triploids from diploids and other types arising from less than perfect effects of the treatment could be a nuisance even to companies specializing in production of polyploids, as would estimating their incidence in seed stock to be sold for grow-out.

The "somatic" procedure entails treatment of either shellfish embryos, larvae, or adults with colchicine or some drug with a similar effect on the mitotic spindle, or cold or heat shock might be used. This would necessitate determining and spot-checking optimal times for treatment, those times the germ-line primordial cells were in active mitosis. If the treatment was successfully applied at the first division of the few presumptive germ-line cells of the embryo, the result should be a totally tetraploid germ line. Effectiveness of the treatment could be quality controlled by simple measurement of gamete size, or unnecessarily by examination of oocyte bivalent chromosome number or chromosome number in the ripening male gonad.

There would have to be some compromise between making the entire germ line polyploid and avoiding polyploidization of too many other cells critical for differentiation. Chances of obtaining a totally tetraploid germ line by treating larvae or adults would be less than for embryos, but other tissues at these life stages would not be as sensitive to the chance polyploidization of cells that happen to be in mitosis at treatment time. Adults should, of course, be treated at the very beginning of their gametogenesis to affect germ primordial cells. This developmental work would have the advantage of the fine research now proceeding in embryology and molecular biology on development of cell lineages, with some particular attention in both vertebrates and invertebrates to the germ-line lineage.

Treated shellfish would, of course, be mosaics. Here this would have the distinct advantage that the normal diploids could support the development of a gonad with not one, but 2 extra chromosome sets. Also, one might seriously consider otherwise that mosaicism was even advantageous.

However this might be, the tetraploid gonad cells of such shellfish should produce diploid gametes. These could be simply crossed with normal gametes to produce triploids without sensitive manipulation of their oocytes.

One cause for the likely poorer survival of triploids produced by manipulating oocytes is the disproportionate chromosome and nuclear to oocyte volume in shellfish eggs with their holoblastic cleavage. Diploid female gametes arising from tetraploid germ-line cells should have the added advantage of a larger size more proportionate to the nuclear and cell sizes of triploid embryos.

Once the optimal basic procedure was developed, more specialized shellfish seed producers could certify stocks they would produce for more general seed producers. Specimens producing only a proportion of tetraploid oocytes, because not all their germ line was affected by the treatment, would simply be sold for less than ones producing almost all tetraploid eggs. Since at least the oyster can live for several years, a few such brood oysters could serve a commercial producer of triploids for several years. Must a producer have only diploid gametes, as for production of all sterile animals, oocytes might be mechanically sorted by size.

The diploid gametes of these shellfish with tetraploid germ lines might be crossed with one another to expand the population, and select out lines of non-tetraploid origin. Provided the totally tetraploid shellfish was vigorous, there would be no need to repeat the experimental treatments of the germ-cell primordia.

Such a procedure could work as well on fish or any other aquaculture groups. Chromosome mosaics have uses!

Likely organismic advantage of mosaics for ploidy level is suggested by a recent paper describing natural occurrence and maintenance of diploid-triploid mosaics in South American populations of a turtle, which further shows geographic variation in occurrence of the mosaics (Bickham J.W. et al. 1985).

Importantly, gynogenetic development of tetraploid eggs would give diploid individuals in oversize eggs which may confer special benefits to the embryos and larvae. Like finfish of tetraploid ancestry, these tetraploids might better tolerate gynogenesis than non-polyploid shellfish.

Should it be possible to make a functional inter-species hybrid of a shellfish with sufficient chromosome differences to inhibit their meiotic pairing, this method could be used to produce clones of hybrid, diploid individuals. This would be accomplished by using irradiated, genetically inactivated sperm. Because maternal and paternal chromosomes would not pair in prophase of meiosis, only bivalents would be formed, and only between the artificially duplicated, genetically identical chromosomes; hence, there could be no random assortment of chromosomes. Also, any meiotic irregularities resulting from quadrivalent pairing of the tetraploid chromosomes would be avoided. Fusion with the second polar body would yield tetraploid clones.

It might not even be necessary to use a hybrid to prevent random assortment of the four sets of maternal and paternal chromosomes. It is conceivable that minor differences in the parental chromosome sets of the same species would be recognized so that pairing was relegated to the perfectly identical partner created by artificial doubling of the germ-line chromosomes. This could be determined in several ways. If pairing were only between these totally identical, artificially duplicated chromosomes, gynogenetic fertilization of the eggs from the tetraploid germ lines would yield diploid genetic replicas of the non-inbred, non-hybrid, but heterozygous sole parent, and forced fusion of the female pronucleus with the second polar body, tetraploid clones.

Finally, any large-scale commercial production of induced polyploid or gynogenetic shellfish could well lead to the discovery of meiotic mutants of use in developing naturally parthenogenetic strains of shellfish through suppression of the segregation division of meiosis. Insofar as performance for important commercial characteristics is determined genetically, natural production of such clones could be of great advantage in shellfish culture. Superior non-inbred genotypes might then be replicated indefinitely with no artificial manipulations at all. Use of polyploids and hybrids would compensate some in artificial culture for reduced genetic diversity resulting from such asexual reproduction as it has in nature. See Figure 10.

PART THREE

CONCLUSIONS

Cytogenetics is presently providing important new information on genetic variability and powerful new methodologies central to the science of genetics and applicable to shellfish studied either as a natural resource or as hatchery-bred populations. For several reasons, cytogenetics could play a role in shellfish breeding similar to the one it has played in plant breeding. Further development of cytogenetics will be critical in applications of recombinant DNA technology to practical breeding goals. Gross chromosome alterations may be important in the domestication process of shellfish. Shellfish have several characteristics making them desirable candidates for chromosome manipulations of various sorts. Chromosome engineering is not exclusive of other genetic breeding techniques but complementary. It is most powerful used in concert with them and, for the future, in concert with recombinant DNA methodology.

Triploid shellfish produced by manipulation of oocytes may have direct commercial use because of their partial sterility, and may be reliably produced commercially. However, alternate production through initial doubling of the chromosome number of the germ line should be considered for production.

By combining hybridization and polyploidy in shellfish, chances are optimized for developing naturally parthenogenetic strains of non-inbred individuals of vastly superior commercial performance, whether for disease resistance, growth or any other character. Also, tetraploidy could lead to direct production of non-inbred clones of outstanding genotypes through induced gynogenesis and polyploidy.

Chromosome segments, genes, whole chromosomes, or chromosome arms might be transferred from non-commercial types with particular desirable genes into commercial types lacking them. Manipulation of shellfish chromosomes might further lead to rapid production of homozygous lines for crossbreeding, for basic studies, and also for other types of research.

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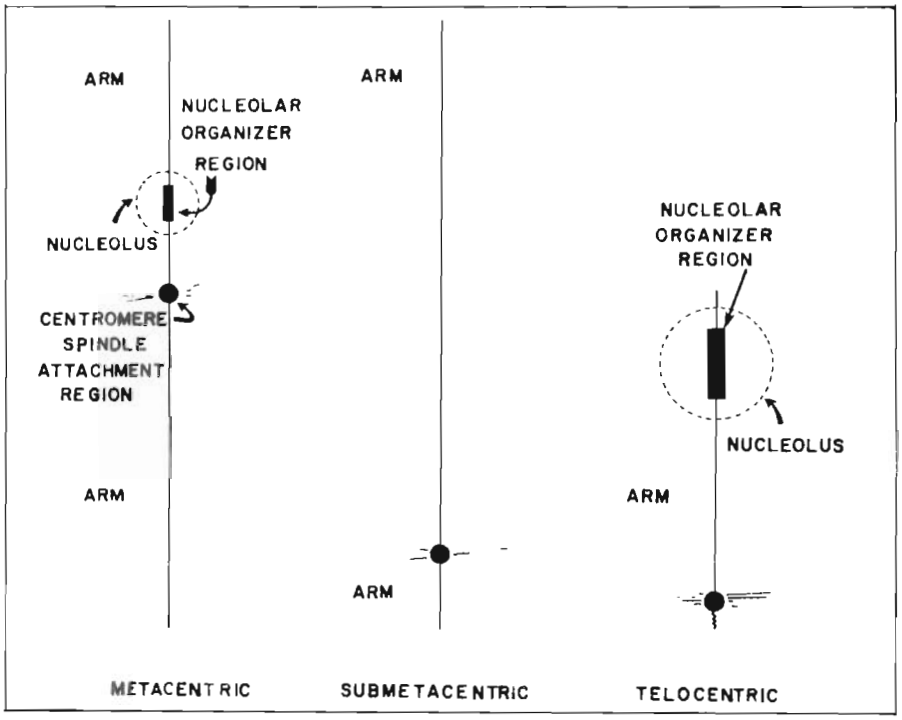
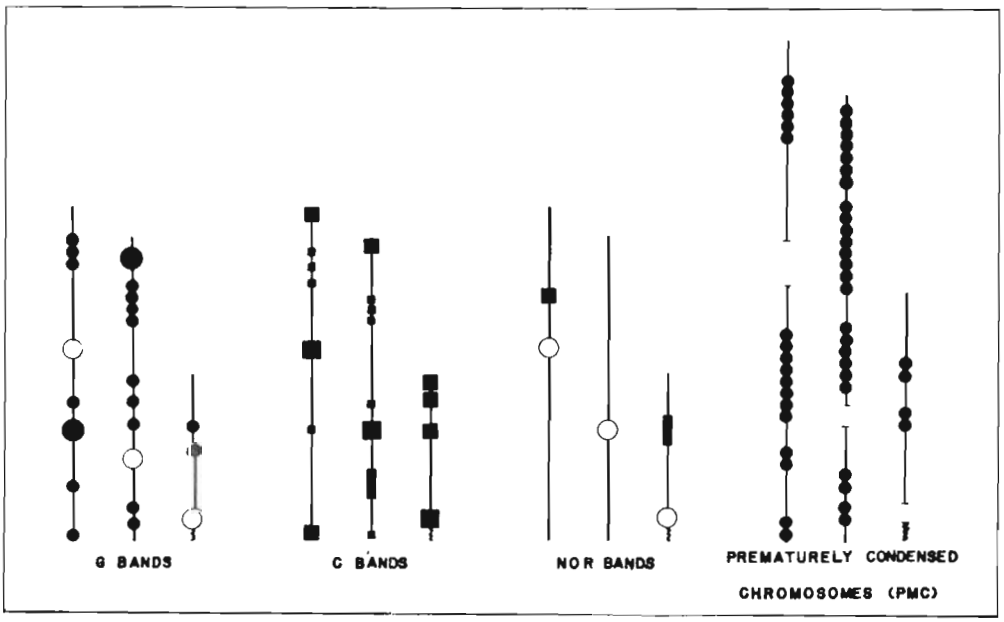


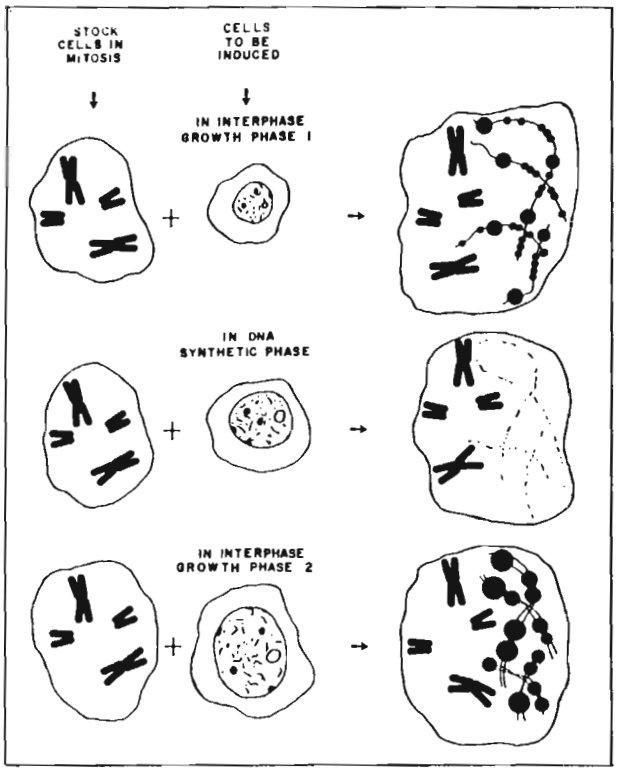
Centromere divides chromosomes into either 2 equal or unequal arms, or occurs very near chromosome end.

Figure 1. Basic features simply observed in eucaryotic chromosomes.



With different chromosome banding procedures now available 3 basic chromosome types illustrated in Figure 1 can be more critically characterized. G bands tend to be interstitial and correspond with chromomeres. C bands correspond to classic heterochromatin, occur at centromeres, chromosome ends, and nucleolar zone. NOR bands occur at nucleolar organizer zones which transcribed messages for ribosomes during last cell cycle. More bands occur in prematurely condensed chromosomes, and tend to be subdivisions of G bands.

Figure 2. Diagrammatic differences between G, C, NOR and PMC banding.



When non-dividing cells are fused to cells in mitosis result is premature contraction of chromosome material of interphase nuclei. Depending upon growth stage of the non-dividing nucleus, its prematurely condensed chromatin occurs in different states with larger or smaller number of bands. To facilitate comparisons to Figures 1 and 2 the same 3 diagrammatic chromosomes are shown here. Adapted from M. R. Ringertz and R. E. Savage, 1974, in Somatic Cell Hybridization, Eds. R. L. Davidson and F. de la Cruz. Raven Press, New York.

Figure 3. Induction of premature chromosome condensation after fusion of non-dividing cells with mitotic cells.

Using either DNA to DNA or DNA to RNA in situ hybridization techniques, location of repetitive DNA on chromosomes can be routinely determined and, with more difficulty, that of particular unique sequences. With such procedures, the idealized 3 chromosomes of prior figures might appear as shown here. Most highly repetitive DNA occurs in nucleolar zones, and moderately repetitive DNA at C band or heterochromatic regions. Highly repetitive chromatin designated here as HR; moderately repetitive, MR; unique sequence, US.

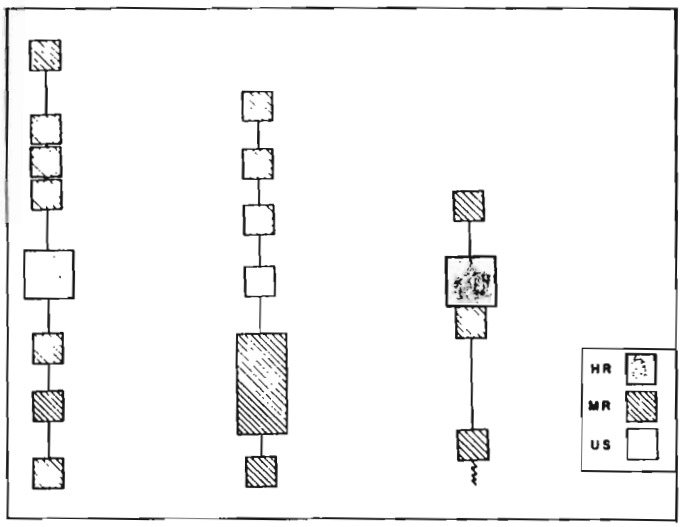
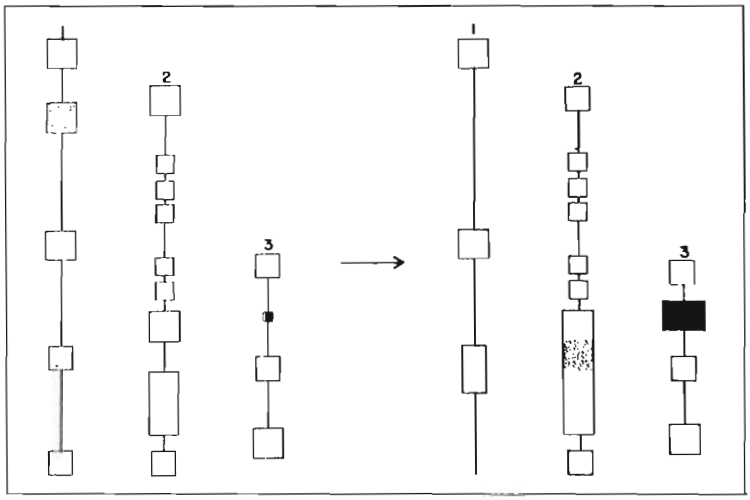
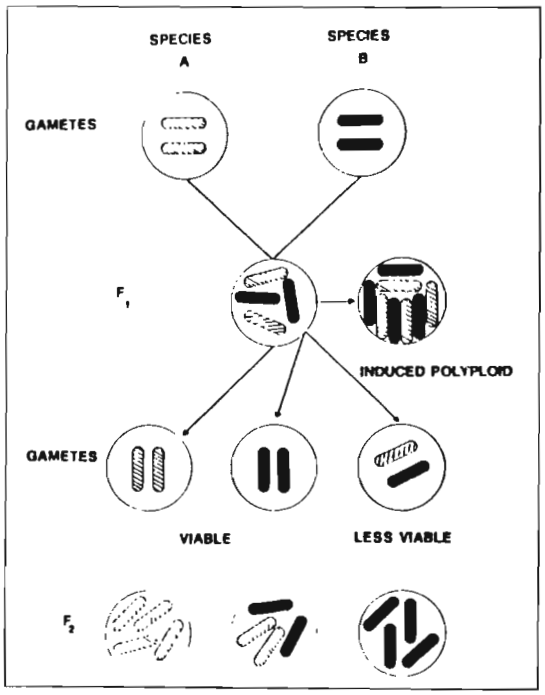


Figure 4. In situ hybridization patterns showing highly and moderately repetitive DNA, and unique sequence DNA.



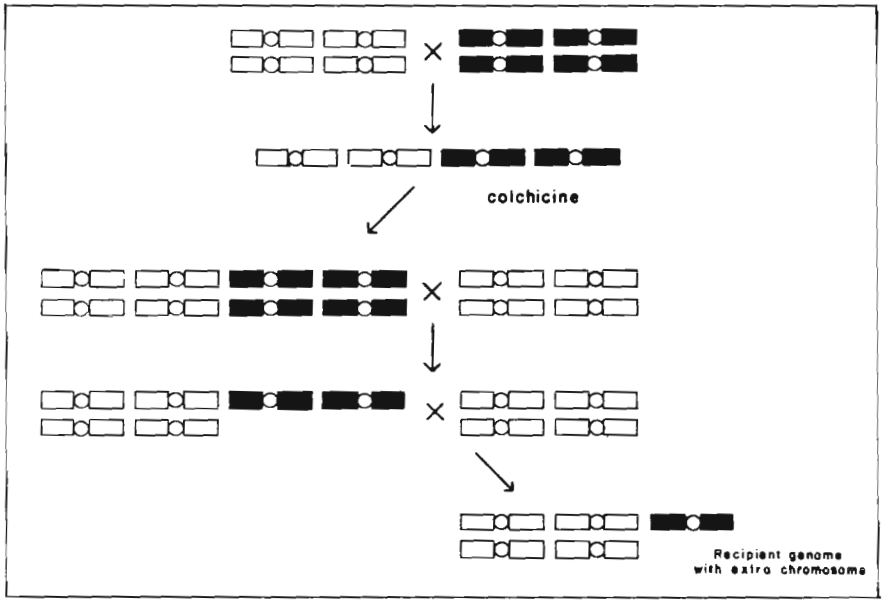
Again using the 3 basic chromosomes as models, examples of potential types of alteration of C bands under influence of mobile genetic elements is shown here. All blocks on chromosomes stand for C bands. As a demonstration, mottled block of chromosome 1 in the group of 3 unaltered chromosomes to the left is shown to be re-located to chromosome 2 in group of 3 altered chromosomes to right of diagram. The third large C band to lowermost end of chromosome 2, as illustrated on left, is shown to move to inserted C band from chromosome 1. A second phenomenon associated with mobile genetic elements, movement of C band heterochromatin along the same chromosome, is illustrated here for chromosome 1 where the terminal, lowermost band is shown to have moved away from its chromosome end and fused with its nearest C band. Third phenomenon associated with mobile genetic elements is demonstrated by amplification of the tiny C band illustrated on chromosome 3 on the left.

Figure 5. C banding under influence of mobile genetic elements.



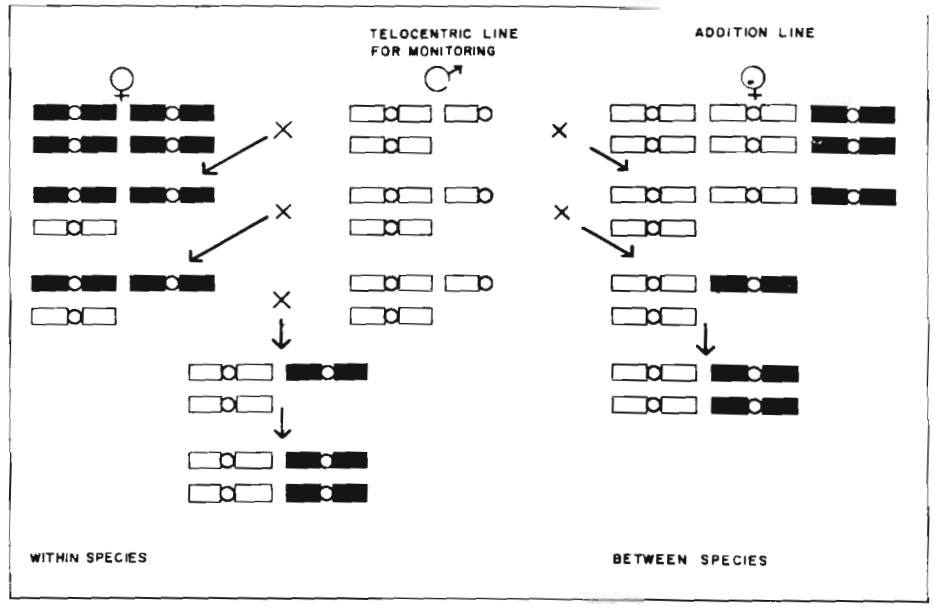
Even in species hybrid crosses where there is induced tetraploidy to circumvent problems in chromosome pairing, there is a tendency for gametes with a mix of chromosomes from either hybrid parent to be less viable than those with a chromosome set exclusively from one or the other parent. Result is a marked divergence towards parental types. Modified slightly from R. S. Caldecott, 1961, in Germ Plasm Resources, Ed. R. E. Hodgson, Publ. No. 66, Amer. Assoc. Adv. Science, Washington, DC.

Figure 6. Divergence of chromosomes towards parental type in inter-specific hybrids.



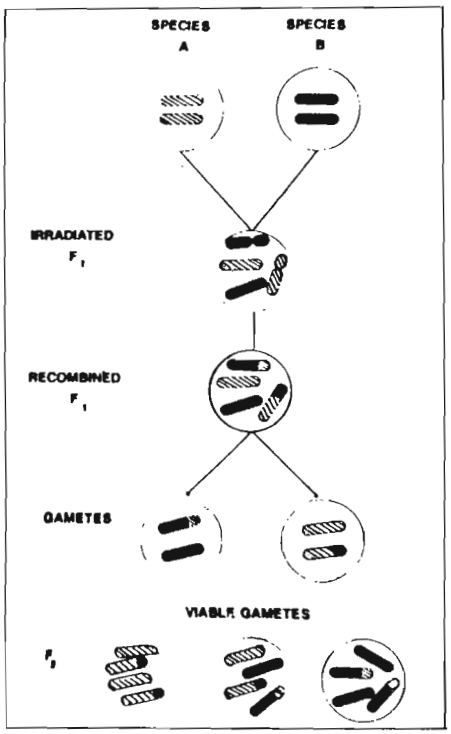
To develop a chromosome addition line or strain two parental lines or species are crossed, and F_1 progeny doubled to make a tetraploid. Tetraploid is backcrossed to generally better adapted parent to yield a triploid which is then backcrossed with adapted diploid parent. Because of abnormal pairing and faulty chromosome segregation with chromosome loss, diploid progeny segregate out with one extra chromosome from foreign strain or species. As adapted from C. N. Law, 1983, in Genetic Engineering, Principles and Methods, Vol. 5, Eds. J. K. Setlow and A. Hollaender, Plenum Press, New York.

Figure 7. Development of a chromosome addition line or strain.



Using an aneuploid line monosomic for a telocentric of the chromosome bearing the gene to be transferred, this diagram shows to the left steps in development of a within-species chromosome substitution line or strain. On the right are shown steps in development of a between-species substitution line or strain. Following first the development of the within-species line, note that the telocentric monosome is conveniently lost so F_1 progeny are monosomic for this chromosome pair. As crosses to the unstable telocentric line are repeated, one can select for progeny which have replaced the normal counterpart of the telocentric chromosome from the alien parent with the chromosome of the standard variety, strain or species. This will first occur as a monosome, but abnormal segregation of unpaired monosome will give rise to a normal diploid number for the substituted chromosome. When breeding between-species substitution lines, a chromosome addition line, the development of which was shown in Figure 7, is crossed with the telocentric line. F_1 progeny are monosomic for both telocentric and addition chromosomes. Crossed again to the telocentric line, F_2 progeny can be selected which have lost one chromosome, and have a single addition line chromosome substituted for the regular species chromosome which is monosomic and unstable. Diploid substitution lines can be selected from progeny of these unstable types. As adapted from C. N. Law, 1983, in Genetic Engineering, Principles and Methods, Vol. 5, Eds. J. K. Setlow and A. Hollaender, Plenum Press, New York.

Figure 8. Development of inter-species and intra-species chromosome substitution line or strain.



Another technique incorporating both hybridization and polyploidy is use of radiation to transpose pieces of chromatin bearing useful genes from a chromosome of one hybrid parent into a chromosome of the other hybrid parent. Unreduced gametes of tetraploid F_1 are irradiated, chromosomes broken and transposed at random. Among viable gametes should be some which carry small portions of chromatin carrying the desired gene in a chromosome set otherwise comprised of the better adapted parent. F_2 progeny are selected on basis of tests for activity of the transferred gene, and also on basis of overall performance. Based on work of E. R. Sears as presented by R. S. Caldecott, 1961, in Germ Plasm Resources, Ed. R. E. Hodgson, Publ. No. 66, Amer. Assoc. Adv. Science, Washington, DC. Copyright 1961 by AAAS.

Figure 9. Use of radiation to transpose chromatin from one genome to another.

To utilize fully potentials of chromosome engineering and molecular biology it is essential that aquaculture breeding have, as its base, fundamental science interacting with applied research to develop breeding programs for producing strains then field- and/or hatchery-tested before progeny are multiplied for marketing. As given by R. H. Lawrence, Jr., Agrigenetics Corporation, panelist in Roundtable Discussion on Research Priorities, 1983, in Genetic Engineering in Plants, An Agricultural Perspective, Eds. T. Kosuge, C. P. Meredith and A. Hollaender. Plenum Press, New York.

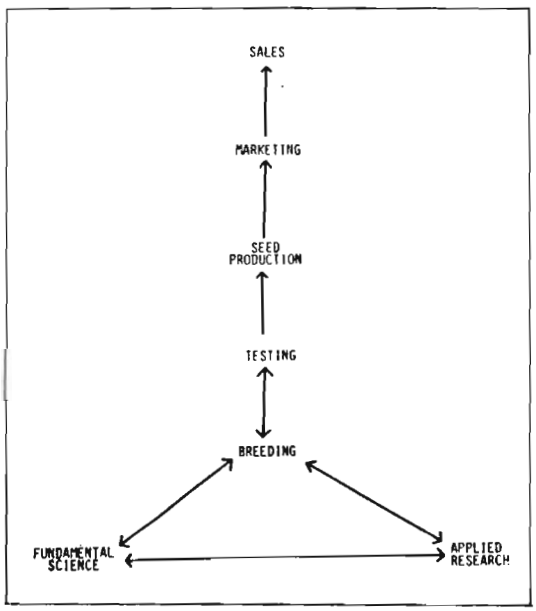


Figure 10. Activities of a fully integrated "seed" company.

SUMMARY OF TECHNOLOGY SESSION

K. CHEW, R.E. LAVOIE *

ABSTRACT

The first paper by CHEW, BEATTIE and DONALDSON discussed bivalve molluscs hatchery techniques, including gonad maturation and the inducement of spawning. In the USA, hatcheries produce approximately 80 % of the Pacific oyster seed on the West Coast and 10 % of the hard clam seed on the East Coast. While establishing a hatchery, the chances for success can be greatly enhanced by close attention to the choice of an appropriate technology and site, to the use of existing proven technology as a base of operations, and by operating outside the normal time of spawning. Careful choice of water supply, broodstock and algal stock is essential. The water supply must be clean either naturally or by the use of a proven and reliable purification system. The algal stock must be free of pathogens and diseases. The broodstock must be clean, healthy and suited to the intended use of the seed. The timing of conditioning and spawning must be adapted to local conditions. Overcrowding during conditioning can reduce or hinder spawning success. Two recent technical advances show much promise to increase hatcheries success : refrigerated pre-produced algal slurry is used as diet supplement for larvae ; remote setting of hatchery larvae reduces hatchery costs and increase seed supply flexibility.

The second paper by LUCAS illustrated the approach used in several hatcheries through several countries. The range of approaches shows much diversity in size, objectives and status of molluscean hatcheries. The casualty list is substantial. Technical problems cause most failures. Problems are frequently environment or animal related. On the environment side, water supply source and treatment processes cause much grief. On the animal side, metabolic, toxic and pathological mortalities are often not determinated and generally poorly documented. A carefully established strategy towards a clear objective would enhance hatcheries success. A hatchery for a naturally collectable species can supplement natural production, buffer the effects of diseases and allow production planning. For a species which cannot be collected naturally, a hatchery can be a precious tool for genetic selection of strains and for development research. In all cases, the establishment strategy should include a biochemical and hydrological analysis of the proposed water supply through a full annual cycle, and possibly the use of mobile hatcheries for site testing. Careful adaptation of techniques to local conditions and target species needs, and increased monitoring and documentation of animal health would go a long way towards making hatcheries a useful and powerful tool in mollusc culture.

The third paper by FLASSCH focused on bivalve pre-growing and grow-out techniques. In the last fifteen years, synthetic materials have brought many new developments. New technologies appear to be adopted more quickly in developing areas than in long established ones because of cultural resistance to change. The intermediate stages (up to 2mm) are grown at high densities ($.5\text{-}5.10^3/m^2$) using overflow and up-flow techniques. Overflow is

* Division of Aquaculture and Invertebrate Fisheries School of Fisheries, University of Washington, **Seattle**, Washington 98195, U.S.A.

Fisheries Research Branch, Department of Fisheries and Oceans, **Halifax**, Nova Scotia, Canada, B3J 2S7

used for oysters, scallops and clams. Up-flow is used for all species except scallops. Intermediate stages are also raised in low densities ($.2\text{-}3.1 \times 10^4/m^2$) on floating and bottom trays and pearl and lantern nets suspended from rafts and long lines. On and in-bottom substrate techniques are also used. Grow-out to market size is done on floating rafts and long lines ; oysters are grown in plastic pouches kept on intertidal bottom trays. Endofaunal species are protected by nets, enclosures, and by predator hindrance techniques. Healthy seed is often key to nursery and grow-out success. Performance assessment of nursery techniques, and a quality standard and labelling system could improve survival to market size and profits. The grow-out techniques selected should ideally have little or no negative impact on animal growth and on the surrounding environment.

DISCUSSION

From a substantial discussion, two pertinent question emerged and elements of answers percolated to the surface. The questions are : 1) are hatcheries needed and why ; 2) if they are needed, how can their survival rate be improved ?

There appears to be wide acceptance of the idea that mollusean hatcheries can be most useful. Several advantages can be listed :
1) They can bring uniformity of production ;
2) They can improve production through genetically selected and improved strains
3) They can allow the culture of species in habitats where natural reproduction does not occur ;
4) They can be very effective once technological limitations have been overcome ;
5) they can be an insurance policy against natural reproduction failures and mass mortalities on the growing sites ;
6) They can be useful research and development tools.

There are disadvantages :
1) They can populate a whole area with poor stock ;
2) They cannot be turned on and off instantly ; trained staff must be maintained and paid continually, specially if the hatchery is to be used as insurance against spatfall failure or for research ;
3) They cost money.

In the final analysis, each country must decide to have them or not, in its own geographical, historical and sociological context. Financing can follow a similar approach. Government can maintain them for the benefit of the collectivity or they can be vertically integrated in large enterprise or financed through consortiums of small companies.

Even though many problems still exist in the area of establishing and maintaining hatcheries either for commercial seed production or for research and development purposes one is left with the impression that the answers to any technological problem can be obtained quickly through access to the expertise available within the group countries. A mechanism for making the expertise available through an international cooperation agreement could indeed be a worthwhile objective for this group.

RÉSUMÉ DE LA SESSION TECHNOLOGIE

K. CHEW, R.E. LAVOIE *

RESUME

La première présentation due à CHEW, BEATTIE et DONALDSON se rapporte aux techniques de production de mollusques en écloserie, y compris la maturation des gonades et l'induction de la ponte. Aux Etats-Unis les écloseries produisent approximativement sur la côte ouest 80 % du naissain de C.gigas et sur la côte est 10 % du naissain de Mercenaria mercenaria. Pour augmenter les chances d'un bon fonctionnement ultérieur, l'implantation d'une écloserie nécessite une attention particulière dans le choix d'une technologie et d'un site approprié, l'utilisation de technologies de bases déjà éprouvées et une production en dehors des périodes normales de ponte. Un choix soigneux de l'alimentation en eau, du stock de géniteurs et d'algues est essentiel. L'eau doit être soit naturellement propre soit purifiée par un système ad hoc. Le stock d'algues ne doit pas être parasité. Les géniteurs doivent être propres, sains et appropriés à la production voulue de naissain. La période de conditionnement et de ponte doit être adaptée aux conditions locales. Une surpopulation pendant le conditionnement peut réduire ou nuire à la ponte. Deux récentes techniques sont prometteuses : des algues produites à l'avance, concentrées en paton et réfrigérées sont utilisées en supplément de nourriture pour les larves ; la commercialisation de larves oeillées aux entreprises de grossissement, qui réalisent elles-mêmes les opérations de fixation, réduit les coûts de l'écloserie et accroît la souplesse de l'approvisionnement.

La deuxième présentation, faite par LUCAS, illustre les stratégies utilisées par plusieurs écloseries dans différents pays. La variété des exemples montre beaucoup de diversité dans la taille, dans les objectifs et dans les statuts des écloseries. Le nombre des fermetures est important, la majorité des échecs résultant de problèmes techniques. Les problèmes sont fréquemment en rapport avec l'environnement ou avec l'animal. Parmi les paramètres d'environnement, l'origine de l'eau et son traitement sont responsables de beaucoup d'accidents. Les causes de mortalités massives d'animaux, liées au métabolisme, à la toxicité et à la pathologie sont souvent indéterminées et peu de documents existent sur ces points. Une stratégie soigneusement établie en vue d'un objectif clair devrait accroître les chances de succès de l'écloserie. Elle peut suppléer à l'approvisionnement d'espèces collectées dans la nature, réduire les effets des maladies et permettre de planifier une production. Pour les espèces, dont le captage naturel n'est pas maîtrisé, l'écloserie est un précieux outil pour la sélection de souches et pour le développement de recherches. Dans tous les cas, la stratégie d'implantation devrait inclure des analyses biochimiques et hydrologiques de l'eau à utiliser, pendant un cycle annuel, et peut-être l'essai du site à l'aide d'une écloserie mobile. Une bonne adaptation des techniques aux conditions locales, les besoins en espèces bien ciblées, un accroissement des données et du contrôle de la santé des animaux devraient permettre à la longue de faire des écloseries un outil utile et puissant pour la conchyliculture.

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* Division of Aquaculture and Invertebrate Fisheries School of Fisheries, University of Washington, **Seattle**, Washington 98195, U.S.A.

Fisheries Research Branch, Department of Fisheries and Oceans, **Halifax**, Nova Scotia, Canada, B3J 2S7

La troisième revue faite par FLASSCH est centrée sur les techniques de prégrossissement et de culture des bivalves. Au cours des 50 dernières années, les matériaux synthétiques ont occasionné de nombreux développements originaux. L'implantation de nouvelles technologies s'effectue préférentiellement dans les centres d'élevage récents, les centres traditionnels faisant preuve d'inertie face au changement. Les juvéniles (jusqu'à 2 mm) croissent à de fortes densités ($0,5-5x10^5$/m2) grâce aux techniques d'"overflow" et d'"up flow". L'"overflow" est utilisé pour les huîtres, les coquilles St-Jacques et les palourdes. L'"up-flow" est employé pour toutes les espèces à l'exception des coquilles St-Jacques (Pectinides). Les juvéniles sont aussi élevés à faible densité ($0,2-3,1x10^4$/m²) dans des claires, en suspension ou sur le sol, et en mer, dans des lanternes japonaises mises en filière sous des radeaux ou des longues-lignes. L'élevage jusqu'à la taille commerciale est pratiqué sous radeaux ou longues-lignes. Les huîtres croissent également dans des poches en plastique posées sur des tables situées en zone intertidale. Les espèces fouisseuses sont protégées des prédateurs par un filet, par des enclos et par divers autres techniques de protection. Un naissain en bonne santé est souvent la condition pour de bons nourrissage et élevage. L'évaluation des performances des nourriceries, la normalisation de la qualité et un système de label pourraient améliorer les résultats des élevages et les gains. Des techniques d'élevage bien choisies devraient engendrer peu ou pas d'impact négatif sur la croissance et sur l'environnement.

DISCUSSION

D'une discussion approfondie sont ressorties deux questions pertinentes, et des éléments de réponse se sont fait jour. Ces questions sont :

1) les écloseries sont-elles nécessaires et pourquoi ? 2) si elles le sont, comment assurer leur survie ?

L'idée que les écloseries de mollusques peuvent être très utiles semble être tout à fait acceptée. Il en ressort plusieurs avantages :
1- Elles peuvent amener une régularité de production.
2- Elles peuvent contribuer à l'amélioration de la production grâce à la création de souches génétiquesplus performantes
3- Elles peuvent permettre la culture d'espèces dans des sites où la reproduction naturelle n'a pas lieu.
4- Elles peuvent être très efficaces une fois les difficultés techniques surmontées.
5- Elles peuvent représenter une garantie contre les défaillances de la reproduction naturelle et contre les mortalités massives dans les sites d'élevage.
6- Elles peuvent être un outil utile pour la recherche et le développement.

Les inconvénients sont :
1- Elles peuvent induire un peuplement avec des souches médiocres.
2- Elles ne peuvent pas être ouvertes ou fermées rapidement ; un personnel qualifié doit être maintenu et payé en permanence, spécialement si l'écloserie doit être utilisée comme un recours en cas de manque de naissain naturel, ou pour la recherche.
3- Elle coûtent de l'argent.

De l'analyse finale il ressort que chaque pays doit décider de l'implantation d'écloseries selon son contexte géographique, historique et sociologique. Le financement peut découler d'une approche semblable. Le gouvernement peut les maintenir pour le profit de la collectivité où elles peuvent être intégrées dans de grandes entreprises ou financées par des consortiums de petites entreprises.

Malgré le fait qu'il existe encore des problèmes dans les écloseries établies et maintenues, soit pour la production commerciale de naissain soit à des fins de recherche, il semble bien que les réponses à certains problèmes technologiques peuvent être obtenues rapidement avec l'accès aux connaissances disponibles à l'intérieur du groupe. Un système de diffusion des données, dans le cadre d'une coopération internationale, pourrait être un objectif intéressant pour le groupe.

BIVALVES MOLLUSCS HATCHERY TECHNIQUES, MATURATION AND TRIGGERING OF SPAWNING

K.K. CHEW,* J.H. BEATTIE,* J.D. DONALDSON **

ABSTRACT

The basic approach to hatchery maintenance, conditioning (gonadal maturation) of breeding stocks, and spawning of bivalve molluscs is well understood and has been described in several publications. Changes have taken place over the past few years primarily in the area of developing better equipment and improving techniques to handle the brood stock, algal stock, and larval culture to ensure best growth and survival. No hatcheries are alike and each is unique in its own location.

The requirements of quality seawater in a hatchery include filtration and sterilization methodology. Prevention and management of bacterial infections is an important part of water quality consideration.

Bivalve molluscs brought into the hatchery for conditioning and subsequent spawning must be vigorous and healthy with a high condition index value. Supplementary feeding during feeding is important to maintain health of the stock and to produce more gametes. Time required for conditioning will depend upon the season and level of gametogenesis and temperature of the conditioning system. In general, there is a direct relationship between the health and condition of brood stock and ultimate survival rate of bivalve larvae.

Various techniques can be used to initiate spawning. Although chemicals have been tried with success, abrupt temperature changes (thermal shock) using sperm or egg suspension is successful with many species. Proper conditioning is probably the single most important factor in successful spawning.

Several publications are available describing larval and algal culture procedures. As a rule for feeding, the density of algal food in the larval tanks should simulate as closely as possible natural densities in the environment.

The use of different algae species depends on preferences and needs within each hatchery. Latest activities are directed to the use of centrifuged algae in the form of a concentrated paste or algal slury as a means to permit year-round availability of algae to feed the larvae hatchery in the United States could be using algal concentrations within the next five years.

The remote setting of eyed Pacific oyster larvae is a new concept which has attracted great interest over the past few years. At least 27 oyster companies along the Pacific coast have built setting tanks. Eyed larvae are shipped from the hatcheries to these individual oyster farmers for setting in their tanks. This procedure has grown in acceptance and is being tried with other species.

* Division of Aquaculture and Invertebrate Fisheries School of Fisheries, University of Washington, **Seattle**, Washington 98195, U.S.A.

** Coast Oyster Company, **Quilcene**, Washington 98376, U.S.A.

RESUME : Les principes de fonctionnement des écloseries, du conditionnement (développement des gonades) des stocks de reproducteurs, et de la ponte des mollusques bivalves sont bien connus et ont été décrits dans plusieurs publications. Des modifications ont été apportées depuis quelques années en priorité pour améliorer la technologie et les méthodes de manipulation des reproducteurs, de production d'algues, et d'élevage larvaire pour assurer les meilleures croissance et survie. Toutes les écloseries sont différentes et chacune est unique dans son site.
Les besoins en eau de mer de bonne qualité d'une écloserie nécessitent des filtrations et des stérilisations. La prévention et la lutte contre les infections bactériennes sont un élément essentiel de la qualité de l'eau.

Les mollusques bivalves amenés dans l'écloserie pour être conditionnés et ensuite mis à pondre doivent être vigoureux et en bonne santé avec un index de condition élevé. Une alimentation d'appoint est très importante pour le maintien de la santé du stock et la production de nombreux gamètes. Le temps nécessaire au conditionnement dépendra de la saison et de l'état de maturité, et de la température dans les enceintes de conditionnement. En général, il y a une relation directe entre l'état de santé et de maturité des reproducteurs et la survie larvaire finale.
Différentes méthodes sont utilisables pour déclencher la ponte. Bien que des produits chimiques aient été essayés avec succès, de brusques changements de température (choc thermique) et des suspensions de sperme ou d'oeufs suffisent pour de nombreuses espèces. Un bon conditionnement est probablement le point le plus important pour une bonne ponte.

Plusieurs publications décrivent les méthodes d'élevage larvaire et de culture d'algues. La règle pour l'alimentation est que la densité algale dans les bacs d'élevage larvaire doit être aussi proche que possible de celle du milieu naturel. L'utilisation de différentes espèces d'algues dépend des préférences ou des besoins de chaque écloserie. Les derniers développements sont orientés vers l'utilisation d'algues centrifugées sous forme de concentrés pâteux ou de gâteaux d'algues, qui assurent une disponibilité tout au long de l'année pour pouvoir nourrir les larves à la demande. Si cette tendance se confirme, on peut prévoir que toutes les écloseries des Etats-Unis utiliseront des concentrés d'algues d'ici cinq ans.

La fixation sur site de larves oeuillées d'huîtres du Pacifique est une méthode nouvelle qui a provoqué un grand intérêt depuis cinq ans. Au moins 27 établissements ostréicoles le long de la côte du Pacifique ont construit des bacs de fixation. Les larves oeillées sont expédiées par les écloseries à ces établissements pour être fixées dans leurs propres bacs. Cette méthode est de mieux en mieux admise et est essayée pour d'autres espèces.

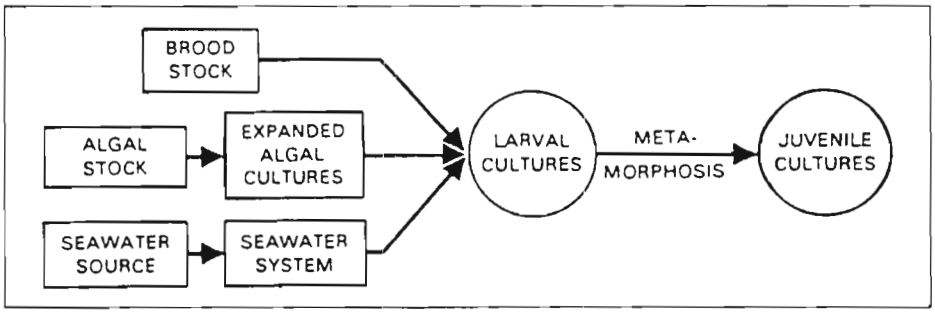

Figure 1. Conceptual diagram of an intensive mollusc husbandry system. (From Elston, 1985)

INTRODUCTION

From an historical point of view, hatchery development in molluscan culture might be said to have begun before the turn of the century. Brooks (1890) in 1879 successfully cultured the larvae of Crassostrea virginica, the native American oyster at Crisfield, Maryland in the United States. Of course other key researchers have contributed greatly to hatchery development since then as noted by Mann (1984); notable prominent names are Winslow, Kimmerer, Bouchon-Brandeley, Cole, Walne, Loosanoff, Dupuy, Castagna, and Breese, among others. Above all, development of hatcheries for mollusc cultivation did not reach the forefront of need until about 25 to 30 years ago. This is especially true for the United States, with which the authors of this paper are most familiar.

This presentation is to highlight the molluscan hatchery techniques, including maturation and mechanisms for spawning. Emphasis will be given to some of the trends in the U.S. With several countries represented at this special international seminar on shellfish culture, we hope to get some interaction or discussions on the latest hatchery innovations and techniques from other countries.

Mollusc production constitutes only 4.6% of the total U.S. production of marine fishes, crustacea, and mollusc (Table 1). Although molluscan production is relatively low, the price of its products is considered very important economically; having a net worth of approximately $336 million in 1983, or 15% of the total U.S. marine fisheries production value. A close review of Table 1 shows oyster and clam production most prominent, with hatcheries playing a role in the production of seed for several of the commercial bivalve species.

Probably the commercial species most dependent on hatchery seed for maintenance is the Pacific oyster (C. gigas). Conservatively, over 80% of Pacific oyster seed is now derived from the hatcheries on the west coast of the United States. Another species somewhat dependent on hatcheries is the hard clam (Mercenaria marcenaria) on the east coast, however hatcheries account for only 10% of the commercial production. Although hatchery seed production of the American oyster (C. virginica) was of importance over earlier years along the northeast coast to the Chesapeake Bay area, it was not considered of vital importance to the maintenance of the fisheries because of natural catches. Several hatcheries in the east produce their own seed of the American oyster for tray and off bottom culture primarily for the half shell trade. With the advent of diseases of C. virginica in the 1950-1960's experimental hatcheries directed efforts to produce disease resistent strains.

Several years ago, the abalone hatcheries in the state of California sell small numbers of juveniles, but lately this has almost ceased. On the Atlantic seaboard few bay scallop (A. irradians) are also sold from time to time for experimental growout but not in significant numbers. Several other species of oysters, clams, and scallops are also dealt within various hatcheries throughout the coastal United States and Canada on an experimental basis.

With the above as background, we will attempt to present what is considered the latest new approaches to hatchery maintenance, conditioning and spawning of mollusc in the U.S. The background emphasis of this presentation might be noted as stated by Mann (1984): 1) to choose appropriate technology for transfer to potential sites and economic climates elsewhere in the world, 2) to use the present technology as a basis for culture of new or old species, and 3) to operate outside of the

time constrictions of natural spawning seasons.

BASIC HATCHERY CONCEPTS

A conceptual diagram of an intensive mollusc husbandry system is taken from Elston (1985) and is presented in Figure 1. The basic elements besides the facility itself are the broodstock, algal stock, and seawater source. It is further recognized that no two hatcheries are alike, and several years of experimentation can be expected before a new hatchery may see some assurance of success. Water quality is quite variable among hatcheries and is often implicated in their problems or failure. Of course, the right people to manage, dedicated workers and continued pursuit of improving old techniques or developing new and innovative techniques are all critical in any hatchery system of operation.

Discussions with successful hatchery managers revealed quite clearly that siting is most important. We know of several molluscan hatcheries which have closed or have had marginal success because the locations in which the hatcheries were built had poor water conditions. Poor areas are usually sites with water of high productivity or uncontrolled low salinities for prolonged periods that can develop partially from heavy rains. Further, these hatchery managers recommend a thorough review of the prospective hatchery sites with respect to target culture species, physical constraints such as ease of pumping water, geological considerations and size of the site, and available energy sources such as electricity and oil and the potential of using alternative energy such as solar or wind.

Once a site is selected, knowledge of other successful hatcheries and their facilities should be at hand before the design of the hatcheries begin. The basic hatchery equipment and operational concepts are available and most shellfish hatcheries are open to fellow farmers and researchers.

Not of least importance is building design that contributes to efficient hatchery operation and ease of cleaning and maintenance.

Hatchery size relates to the resources available to build. All too often insufficient funding pushes a person to plan improperly and hurredly move into production. Most of these impromptu operations do not survive and only a few remain along the coastal United States.

LATEST HATCHERY TECHNIQUES

One would have to follow the total step-by-step process to discern what might be considered latest techniques with equipment or methodologies. Some techniques have not changed for twenty years. Thus, we will present some of our latest views on water source, conditioning (maturation) of shell stock, spawning, larval rearing and algae culture and the remote setting of eyed oyster larvae.

Water Source

The water source that is used for a hatchery can be pumped from the bay or saltwater well, depending on the location. Hatcheries with wells do not need to filter the seawater, but water from a bay needs to be filtered. The most economic way to handle the filtration is with a bag filter (5 or 10 microns) (American Felt and Filter Co., Newberg, New York, 12550). Larger hatcheries use the combination of sand and bag filters in their system. Much depends on the amount of suspended matter, but in most cases the hatchery operations call for the filter bag. In some hatcheries, the filtered water is sterilized with an ultraviolet or ozone system.

When the water is pumped into the hatchery, it is used for algal culture, for conditioning bivalves for spawning, for rearing larvae and the culturing juvenile. For algal culture, filtered water is generally purified by pasteurization or with sodium hypochlorite (minimum of 10 ppm)

for several hours to kill bacteria and phytoplankton and later dechlorinated with sodium thiosulfate before innoculatioon with algae and nutrients.

Water for conditioning adults and larval rearing does not need to be sterilized. Often it contains natural foods that are utilized by the adults and larvae. Water is brought to culture temperature using a heat exchanger.

Finally, in terms of securing the best water quality for the culture of algae and larvae, one has to give serious thoughts to prevention and management of bacterial infections. This is illustrated in Table 2 from Elston (1985). Each of the items in the table requires astute surveillance and regular sanitation procedures to control bacterial buildup within the system. Improper maintenance of a hatchery water system can lead to very serious problems. It is sometimes necessary to close the whole hatchery system and completely sterilize all equipment and facilities before startup. This has happened in several hatcheries and utmost cleanliness and conscientious management of the water source cannot be overemphasized.

Conditioning (Maturation)

The first requirement for conditioning of any species for spawning and rearing under artificial conditions is selection of broodstock. Selection for desired external characteristics is of course important, but selection of meat quality and quantity is equally valuable. It is important to start with a vigorous and healthy animal. Their condition may be judged quantitatively by using the regular condition index of dried meat weight or a more useful tool for commercial hatcheries is to simply sacrifice a few animals in a group and make a visual comparison of meats.

Once animals have been selected, the next step is to produce ripe

gametes. Adequate water quality, food, and the correct temperature are the primary ingredients. If animals are to be conditioned out of season, then they are normally brought into static tanks at or very near the ambient temperature from which they were removed. The temperature is gradually increased over a 5-7 day period up to a few degrees above the temperature at which they would naturally condition. Out of season spawning of all commercially valuable bivalves in the United States (i.e. C. gigas, C. virginica, M. mercenaria, and T. japonica) requires a minimum of 4-6 weeks of conditioning before spawning can commence. It is important to note that a slight increase in conditioning temperature will produce a dramatic shortening of conditioning time. For example, during late winter and spring, Pacific oysters at 22°C require four weeks for completion of gametogenesis, while the same result at 18°C requires eight weeks. Muranaka and Lannan (1984) found that rate of conditioning is a function of temperature intensity and time rather than accumulated thermal units.

If adult animals are conditioned in a static system, they must not be overcrowded. A density of one to two animals for every fifty liters of culture water is desirable. The system should be drained and sterilized every 2-3 days for best results. The animals must have a supplementary food supply in this kind of system. Normally, about 2 liters/animal/day at an algal concentration of 2×10^6 cells/ml is an adequate ration. Feeding is important to maintain the health of the stock as well as to produce more gametes. Supplementary feeding for Pacific oysters as noted by Muranaka and Lannan (1984) produced more gametes, but did not increase survival of offspring. They also found that elevated salinities were preferential to lower salinity levels. Newkirk and Kayarat (1985) found that supplemental lipid for the European flat oysters (O. edulis) broodstock increased fecundity and also increased survival and growth of larvae. Helm et al.

(1973) previously discussed the effects of supplemental algal feeding on hatchery breeding stock of the same species on subsequent larval vigor. Lannan (1980) reported on an optimum conditioning "window" that produces high survival of offspring in the Pacific oyster. The "window" was derived from variations in temperature, salinity, and food supply to obtain the best combination under that particular hatchery's water quality situation for highest survival of offspring. Also, it was interesting to note that Creekman (1977) found that the addition of cornstarch to the broodstock diet increased larval survival. Thus, research studies have shown in general a direct relationship between the health and condition of the broodstock to the ultimate survival rate of larvae.

Spawning

In all cases for the west coast, adult Pacific oysters are brought into spawning condition using a static culture method as indicated above. When they reach a state of gonadal maturity, the oysters can be spawned by increasing the temperature suddenly to 28-32°C and lowering the temperature down to 20°C or leaving them dry for a period of time to initiate the spawning process. This does not always work, but has been fairly successful with the Pacific oyster. Thermal shock at lower temperature levels can also create spawning for the hard clam (M. mercenaria) and the American and European flat oysters in the N.E. region of the U.S. There has been described in the literature many methods of artifically inducing bivalve molluscs to spawn including the temperature shock that was described (Galtsoff, 1940; Kinoshito et al. 1943; Yamamoto 1951; Loosanoff and Davis 1963; Dupuy et al. 1977; Castagna and Kraeuter 1981). Also, the addition of eggs to initiate the males to spawn can be successful at times as well as the popular described method of using sperm suspension (Galtsoff

1940). Other methods are available such as additions of high density phytoplankton (Himmelman 1980; Breese and Robinson 1981), injection of potassium chloride or ammonium chloride (Iwata 1951; Sagara 1958), and/or additions of hydrogen peroxide or ultraviolet irradiated water (Kikuchi and Uki 1974; Morse et al. 1976). One would still have to note that the most common methods of inducing spawning in bivalve mollusc involve temperature shock and addition of gonadal products from adults.

A new method that has recently been developed is for the use of an intragonadal injection of serotonin to induce spawning in bivalve mollusc. Serotonin (5-hydroxytryptamine) creatinine sulfate was first described by Matsutani and Nomura (1982) where they induced spawning of the scallop, Patinopecten yessoensis in Japan. Follow-up work by researchers in the United States have shown positive results in getting most local commercial species of bivalves to spawn. Gibbons and Castagna (1984) were able to show positive results on six different species. However, experiments with serotonin injection in Pacific oysters have not been highly successful on the west coast of the United States although Matsutani and Nomura indicated success with their local Pacific oyster stocks in Japan. The potential use of serotonin to initiate spawning in most bivalves should be examined more closely. One has to consider the practicality of using this chemical because of potential hazards to human health through handling. It is used in the medical field at the present time for therapy and studies related to the human nervous system and its potential danger could be a factor in determining the future use of such a chemical product routinely in the hatchery.

Finally, and most important proper conditioning is the single most important factor in successful spawning. Chemical use for initiating spawning in most species should only be considered as a last resort.

Larval Rearing and Algae Culture

The basic approaches to larval and algal culture of bivalve mollusc are described in several publications (Loosanoff and Davis 1963; Dupuy et al. 1977; Breese and Malouf 1975; Hidu and Richmond 1974; Lipschultz and Krantz 1980). Recent concern with the nursery portion of bivalve mollusc culture was shown when a special conference was called to discuss this issue in Europe, and the proceedings of that meeting have been published (Claus et al. 1981).

Larval culture techniques have not changed a great deal over the years. Tanks must be cleaned and sanitized on a regular basis. The seawater system must be monitored to insure good water quality. In addition, larval nutrition is critical. The number of algal cells available to the developing larvae has to be watched and maintained at a certain level. In this regard, natural food levels must be similated as much as possible. A cell density of 20,000/ml is generally understood to be optimal for developing larvae.

Different hatcheries have different size tanks for rearing larvae. The largest oyster hatchery in the United States, (Coast Oyster Hatchery in Quilcene, of the State of Washington) has switched from the use of 20,000 liter tanks to 40,000 liter tanks. They have shown this process to be more efficient than using small tanks when attempting to grow large numbers of larvae. Similar to other hatcheries, they have established that it is best to grow larvae through straight hinge size at a density of 2-3/ml and switching over to a less dense 1/ml as the larvae approach setting size.

Usually fertilized eggs are stocked at 5/ml until they reach the first veliger stage (24 to 48 hrs). They are then distributed to 40,000 liter tanks, where water is changed every three days. Other hatcheries along the coastal United States have other systems for handling the larvae, but the

basic approaches and procedures are the same; siphon the larvae onto a screen, clean the tank, refill the tank, examine a sample of larvae microscopically, return the larvae to the tank. In a general review of hatcheries in the United States, the larger east coast facilities strive to grow fewer larvae in proportion to the size of facilities because their principle operation is to develop juveniles for the nursery. However, on the west coast the two larger hatcheries for Pacific oyster seed, Whiskey Creek Oyster Farm in the State of Oregon, and Coast Oyster Company in the State of Washington, rear large quantities of larvae for remote setting. The concept of remote setting will be discussed at a later part of this paper. Coast Oyster Company is vertically integrated from hatchery through harvest, and thus produces large amounts of seed for nursery and growout.

The basic requirements for an algal culture system are described by Dupuy et al. (1977). However, some modifications have taken place in recent years hatcheries to produce a high volume of unicellular algae. Using the example of Coast Oyster Company Hatchery again, the move is now toward the use of larger tanks for batch culture. Beginning with a starter culture of 500 ml in a 1,000 ml flask, and transferring to successively larger vessels at 1 to 2 day intervals; a 20 liter carboy, to a 3,000 liter tank and subsequently a 20,000 liter tank, a large amount of food can be produced in a short period of time. This cycle takes only 6-8 days at 20 C. Thus, the turnaround time is rather rapid, and they have found this system to be the best for them. It should also be noted that illumination is important. They found it best tc have the 20,000 liter tanks fitted with 1,000 watt-metal arc or high pressure sodium lamps 2 to 3 feet over the water. Both are high intensity discharge (HID) lights which emit wave lengths desirable for photosynthesis. Other hatcheries use a variety of

lighting ranging from a battery of flourescent day-light type fixtures to regular light bulbs of high wattage, and sunlight.

It should be noted here that much larger algal tanks to 40,000 liters are used for mass algal culture for nursery operations as done at Aquaculture Research Corporation (ARC) in Dennis, Massachusetts. Large greenhouse facilities at ARC with several of these large sized tanks mass produce algal food throughout the year. During the winter months, HID lights for illumination are needed because of short days and cooler temperatures at this northerly location in the United States.

It appears as if the most popular algal culture food for bivalve larvae for the east coast is Tahitian-Isochrysis, Thalasiosira pseudonana, Skeletonema costatum, Tetraselmis suecica, and Chaetoceros gracilis. For the west coast the three main types of algal culture for the larvae are Tahitian-Isochrysis, Thalasiosira pseudonana, and Chaetoceros calcitrans. A variety of other species are also grown under monospecific culture but are not listed here. We should note that these species have been found to be tolerant to wide temperature variations as well as accelerated growth rates. Species used extensively in earlier years such as Pavlora (e.g., Monodugs) and Isochrysis galbana are not now used as extensively because of low growth rates and fastidious growth requirements. Hatcheries can use single species or a combination of species to feed the larvae, depending on individual preferences and needs within each hatchery.

Larval food in sufficient quantity can be grown by most hatcheries with larger algal facilities. At times in some hatcheries food demand is greater than algal production capability and represents a bottleneck for that facility. A possible solution to this problem is through the use of algal concentrated paste or algal slury as described by Krantz et al. (1982). Algae cultures are harvested, dewatered with a centrifuge and then

stored in paste form. This technique permits year round availability of algae as feed for larvae, juveniles or broodstock. It is anticipated that some hatcheries will grow algae for centrifuging during the off season. Larvae can then be grown in the same tanks during the summer. It is expected that if the trend continues, every hatchery will be using the algal concentrate within a few years.

Remote Setting of Eyed Larvae

Although this review is primarily on hatchery techniques, maturation and spawning, one would be remiss not to mention the exciting new culture technique for remote setting of eyed oyster larvae which has developed in recent years. During the past three years at least 27 oyster companies along the Pacific coast have built tanks to catch their own Pacific oyster seed from eyed larvae purchased from primarily two private hatcheries (Whiskey Creek Oyster Farm and Coast Oyster Company). Although this concept was tried and discussed over 20 years ago, it has only recently taken hold. One hatchery can produce millions of eyed larvae in any given year. They can be shipped with ease at low cost and have a fairly high success rate for seed settlement on culture material in tanks. The cost of eyed larvae runs under 10 cents/1,000 at the present time. A document describing this concept and facilities involved with remote setting of eyed larvae was published by Jones and Jones (1983). More detailed research was conducted by Henderson (1983) showing the importance of temperature and salinity for the eyed larval settlement. He was able to show that temperatures and salinities in remote settling tanks should be around 30°C and 30 o/oo for optimum results. Also, he was able to show that Pacific oyster larvae stored at 5°C should not be held beyond eight days for best larval settlement and survival of the newly set seed.

The amount of seed produced in the State of Washington using this technique has jumped from less than 5,000 cases in 1980 to approximately 19,000-20,000 cases in 1982 and was estimated to be 50,000-60,000 cases in 1984. (There are approximately 15,000-20,000 Pacific oyster spat or seed per case. This measurement was established during the period when large quantities of Pacific oyster seed were purchased from Japan and shipped to the west coast of the United States for growing).

Remote setting of eyed larvae with the American oyster (C. virginica), Olympia oyster (O. lurida) and European flat oyster (O. edulis) have also been tested. Eyed larvae of European flat oysters are being shipped to Europe for test setting.

SUMMARY

Successful hatchery techniques have been implemented. The following points have been crucial to this success.

1. Water quality through site selection and water system maintenance.
2. Conditioning of broodstock to ensure larval success, based on static system and supplemental feeding.
3. Spawning induced by thermal shock and stimulation by gonadal products.
4. Insurance of sufficient quality food for broodstock, larvae and juveniles through greatly expanded batch algal culture, and production of a centrifuged algal paste.
5. Larval production has been expanded by use of the technique of remote setting of eyed larvae. This allows a centralized facility to distribute larvae for setting over a wide geographic area.

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Table 1. Estimated Five Year Average (1978-1982) of Commercial Landings for Mollusc in the United States

	Metric Tons (Meat weight)
Oysters	
Pacific *Crassotrea gigas*[1]	2,950
American *Crassostrea virginica*[2]	27,400
Others	50
Oyster Total	30,400
Clams	
Hard: *Mercenaria mercenaria*[1]	6,325
Surf: *Spisula solidissima*	18,850
Ocean quahog: *Arctica islandica*	14,740
Soft: *Mya arenaria*	3,970
Manila: *Tapes japonica*[2]	500
Others	1,315
Clam Total	45,700
Scallops	
Bay: *Argopecten irradians*[1]	595
Calico: *Argopecten gibbus*	2,490
Sea: *Placopecten magellanius*	12,960
Others	5
Scallop Total	16,050
Others	
Squids, Octopus, Abalone[2], Mussels	42,200
GRAND TOTAL	134,350[3]

[1]Dependent on hatchery seed for portion of commercial production.

[2]Seed produced in the hatchery and sole regularly or irregularly to commercial shellfish growers.

[3]Estimated average 5 year total of commercial marine landings of all species of fish and crustacea (round or live weight) and mollusc (meat weight) is 2,920,000 M.T.. Mollusc is only 4.6% of the total production.

TABLE 2. Prevention and Management of Bacterial Infections

Maintain pathogen-free algal stocks and expanded cultures.
Maintain absence or low levels of vibrios in the system (water column and surfaces).
—Use appropriate degree of water filtration.
—Maintain hygiene of system surfaces.
—Use appropriate frequency of water changes.
Isolate infected stocks and associated equipment at first sign of clinical disease.
Discard infected stocks and sterilize equipment.
Identify source of infectious organisms, and modify and clean system.

From Elston (1985)

DEVELOPMENT STRATEGY FOR BIVALVE HATCHERIES

A. LUCAS *

ABSTRACT : Development strategy for bivalve hatcheries is analysed from a sample limited to production hatcheries, and for technical aspects only. For the 30 hatcheries which were referenced, it has been found a wide variety of status (state or private) activity (yearround or seasonal), size and type of products (eyed larvae, set seed or free spat). For these reasons causes of failure, which are still frequent, are difficult to analyse. Nevertheless, mortalities occuring during rearing (which increase production cost and make output unpredictable) have two origins :
- seawater quality (physical and chemical, and bacteriae) at the intake and after treatment ;
- physiological status of larvae and post-larvae (quality of oocytes, metabolism, toxicity, start of metamorphosis).

For both problems, progresses in fundamental research shall give improvements in hatcheries. It would worthwhile to make plans for research on this field, by means of workshops and concerted programs.

RESUME : La stratégie de développement des écloseries de bivalves a été limitée aux écloseries de production et à l'aspect technologique du problème. Sur 30 écloseries ayant servi de référence, on constate que celles-ci montrent une grande variété quant à leur statut (public ou privé), leur activité (annuelle ou saisonnière), leurs dimensions et la nature du produit fourni (larves oeillées, naissain fixé ou naissain libre). Aussi, les causes d'échec, dont la fréquence est encore élevée, sont-elles difficiles à analyser. Cependant, il apparaît que les mortalités d'élevage (qui accroissent le coût de production et rendent incertaine la production) proviennent de deux causes :
- la qualité physico-chimique et bactériologique de l'eau de mer à l'origine et après traitement ;
- la condition physiologique des larves et post-larves (qualité de pontes, métabolisme, intoxication, induction de la métamorphose).

Pour ces deux problèmes, les progrès dans les écloseries résulteront des progrès en science fondamentale. Il conviendrait donc de planifier les recherches à ce sujet en organisant, par exemple, des tables rondes et des programmes concertés.

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* Université de Bretagne Occidentale, Laboratoire de Zoologie,
6 avenue Le Gorgeu, 29287 **Brest** Cedex, France

STATUS	*Public sector: (or semi-public)*	
	Subsidized budget (operating subsidies or government investment)	05. 12. 15. 20. 27. 29. 30.
	Private sector:	
	Independent hatcheries (Manage own budget with or without government subsidies)	03. 04. 07. 10. 11. 19. 21. 22. 23. 24. 25. 28.
	Hatcheries that are part of a shellfish culture operation (common budget)	01. 02. 08. 09. 16.
	Hatcheries that depend on private companies (Subsidized budget)	06. 13. 14. 17. 18.
TYPE OF ACTIVITY	Annual	03. 04. 06. 10. 11. 13. 14. 15. 17. 19. 20. 24. 28. 29. 30.
	Seasonal	01. 02. 05. 07. 08. 09. 12. 16. 18. 21. 22. 23. 25. 27.
SIZE (personnel)	1-3 persons	21. 22. 23. 25. 27. 28. 30.
	4-9 persons	01. 02. 03. 05. 06. 07. 08. 09. 11. 12 14. 15. 16. 17. 18. 19. 20. 24. 29
	10 or more persons	04. 10. 13.
PRODUCT SUPPLIED	Eyed larvae	25.
	Fixed spat	01. 02. 07. 08. 09. 15. 16. 27.
	Free spat	03. 04. 05. 06. 10. 11. 12. 13. 14. 17 18. 19. 20. 21. 22. 23. 24. 28. 29. 30

Table 1: Various types of bivalve hatcheries (production)
Numbers refer to hatcheries listed at the end of this paper.

Commercial hatcheries for bivalve molluscs began operations in the 1960s, following work by LOOSANOFF and DAVIS (1963) in Milford, U.S.A., and WALNE (1956) in Conway, Wales.

The role of these hatcheries has been:

- to cultivate species which were difficult or impossible to capture naturally (in particular hypogeal species such as the Veneridae),

- to remedy shortfalls in natural captures (for example in cases of insufficient fixing or of secondary spat loss),

- to achieve better-planned management through controlled production in hatcheries, possibly based on genetic selection.

This paper will deal only with producing hatcheries, commercial or non-commercial, and thus will not discuss experimental hatcheries, except where these have well-defined production programs. We do not intend to deal with the economic aspect of hatchery development strategies, since we feel that failures have to date been due rather to technical production problems rather than difficulties in marketing the product.

1. CURRENT STATUS AND OBSERVATIONS

1.1 TYPES OF HATCHERIES

As Table 1 shows, there are many different types of producing hatcheries.

1.2 PRODUCTION BY SPECIES AND COUNTRY

Given the diversity of products (Table 1), it is difficult to make a general evaluation. It is impossible to compare the production of eyed larvae and fixed spat with that of free spat.

In 1981, Hatchery 25 announced production of one billion eyed larvae with a guaranteed settlement rate of 20%; however, only a small percentage of larvae that settle on collectors reach the adult stage.

Mortality of free spat is normally quite low, thus explaining the production figures for this type of spat.

In this connection, we may note the following orders of magnitude:

- production in the order of 50 to 100 million free spat for the following species: *Crassostrea gigas*, *Crassostrea virginica*, *Ostrea edulis*, *Tapes philippinarum*, *Mercenaria mercenaria*,

- production of from 1 to several million free spat for the following species: *Pecten maximus*, *Mytilus viridis*, *Pinctada* sp.

Even with such limited production, hatcheries have played a significant qualitative role, as was shown in 1980 for Western Europe (LUCAS, 1981).

The principal producing countries are:

- the U.S.A., which produces *C. virginica* and *M. Mercenaria* on the Atlantic coast (08, 09, 12) and *C. gigas* on the Pacific coast (25). The upswing in production of *Ostrea edulis* in Maine in the early 1980s (21, 22, 23, 24) seems to have diminished recently.

- France produces mainly *Tapes philippinarum* (in rising quantities since 1980) and *Crassostrea gigas* in quantities that vary with spat collections. Most of this production comes from Hatchery 04.

- Great Britain produces a considerable variety: *C. gigas*, *O. edulis*, *M. mercenaria*, *Tapes decussatus* and, starting recently, *T. philippinarum*.

- Tahiti (COP) produces *Mytilus viridis* (Aquacop and de GALLANDE, 1979).

- Japan produces the pearl oyster *Pinctada* sp.

- New Zealand produces *Saccostrea glomerata* (CURTIN, 1979).

With the latter, the variety of species produced is further extended.

As well, several European countries have invested in hatcheries, although so far without great success (e.g. Spain, Ireland).

1.3 FREQUENCY AND CAUSES OF FAILURE

It is impossible to make a thorough analysis of failures, since there has never been an exhaustive account of successful hatcheries. This would, in any case, have been difficult to produce due to the diversity of hatcheries (Table 1). It is nevertheless a fact that there are more hatcheries closed than active, and that closures affect all types of hatcheries.

The opinion expressed by SHAW in 1972 is still valid today: "Although molluscan aquaculture has attracted great interest in recent years, there is still a lack of know-how to make such ventures a commercial success. Many companies have blindly entered the field and have lost enormous amounts of money".

Technological reasons for failure are basically related to the fact that spat production is irregular in many hatcheries. What is more serious is that hatcheries most often cannot determine the causes of mortality, any more than the causes of success.

From a technological standpoint, this is a problem of applied ecophysiology. In the field of ecological physiology, analysis must take into account both the environment and the living organism. This is why we shall deal with these two aspects of the problem separately.

2. STRATEGY WITH RESPECT TO ENVIRONMENT

2.1 SEA WATER QUALITY AT INTAKE: observations

All hatcheries pump in natural sea water, the quality of which before treatment varies from one site to another. This variation may have a considerable influence on larva development, as was shown by WILSON (1951) using Celtic sea water, where the pluteus of sea urchins developed well, and that from around Plymouth, where plutei developed poorly. This was confirmed in the Mediterranean by BOUGIS (1964). Bivalve veligers are organisms that are just as sensitive as sea urchin plutei to the quality of untreated sea water, as shown in the recent example cited below (COCHARD, pers. com.).

Hatchery 29. September 1984. *Pecten maximus*, larvae of same parental origin, all conditions identical except for water source. On 19th day, larval size (in µm) in three tanks for each water source was:

Water pumped from outside breeding ground:	172	175	166
Water pumped from inside breeding ground:	182	188	187

It is entirely possible that the continuing lack of success of certain hatcheries (where one team of biologists after another has failed) is due to the poor quality of sea water at the source. In France, for example, we could mention Hatchery 18 (which pumps in not sea water but "swamp" water), and in the U.S. Hatchery 13, which has its water intake near the outlet of a power station and a plant extracting magnesium from sea water and releasing effluents containing particulate burcite and calcite and which are poor in Mg^{++} ions.

Sea water quality may also vary with the seasons and with weather conditions. WALNE (1970) demonstrated that seawater at Conway was not fit for larva culture following heavy rains bringing about turbidity in the estuary, in spite of treatment (sedimentation, filtration).

To avoid fluctuations in natural seawater quality, many hatcheries have used underground seawater (08, 09, 13), but this "well" water has never been used successfully in raising larva, and can only be used to raise algae and occasionally breeders. And yet this water has a very low bacteria content and exhibits no obvious chemical imbalance.

Artificial seawater, available commercially (e.g. Instant Ocean), is no better for larva raising; however, a new artificial seawater formula, developed by ZAROOGIAN et al. (1969) has been used to grow bivalves (CABLE and LANDERS, 1974).

2.2 SEA WATER QUALITY AT INTAKE: strategies

The problem here is one of choosing a site to build a hatchery, provided such a choice is made for technical reasons and has not been dictated in advance for financial, administrative and/or political reasons.

Most hatchery managers have located their facilities on sites where the seawater appeared to be clean, without any known pollutants and not subject to great seasonal variations. But if we wish to go beyond such an empirical attitude, what are the rational solutions to this problem? There are two possibilities:

1. Preliminary hydrological analyses, although we must first determine which analyses are required. Seawater may be said to be unfit for raising larvae if it is deficient in essential substances or if it contains toxic substances.

At the present time, the majority of these two types of substances are unknown. It may be hoped that rapid progress will be made here using HPLC for detecting free amino acids (MANAHAN and STEPHENS, 1983) and FPLC for proteins, but the list of soluble organic substances is not limited to these two categories.

As well, biochemical analysis of seawater should be carried out over a yearly cycle, given the seasonal variations in water quality.

Certain analyses, even though they are primitive and applied only occasionally, can sometimes indicate the inappropriateness of a site, and use of these should certainly be encouraged.

2. Mobile hatcheries. Given the blind character of hydrological analyses, I once suggested another approach to the Shellfish Association, based on the existence of a light mobile hatchery (LUCAS, 1982a). I stated that "The potential mobility would be of great advantage, as it would permit the search for those sites with the best water quality, or the move to more favourable sites following temporary or long-term marine pollution".

2.3 TREATMENT AND MONITORING OF SEAWATER IN HATCHERIES

2.3.1 Simple strategy: centrifuging seawater

This method, developed by WELLS, consists in centrifuging seawater (thus causing elimination of zooplankton, but not phytoplankton) and then incubating this seawater, under intense light, at a temperature of 18-20°C. Within 2-3 days, an extremely active monocelluar algae bloom of natural nannoplankton is produced. This method, which is simple and economical, is used in Hatcheries 09 and 12, although the results it gives are too irregular, given the differing sites and seasons, to recommend it for general use (LUCAS, 1982b).

2.3.2 Elaborate strategy

There are normally three seawater circuits (using different treatments): for algal culture, for breeders and for larvae. Looking only at the last, the treatments applied are the following:

- elimination of particles by progressive filtration,

- elimination of bacteria by sterilization (e.g. ultraviolet) or by fine filtration (0.2 µm). If required, antibiotics may be added to stop the proliferation of bacteria (BLOGOSLAWSKI et al., 1978),

- heat regulation by use of a heat exchanger,

- various pumping operations and storage in reservoirs for varying lengths of time,

- periodical changing of water in larva tanks (every day, or every 2 or 3 days, depending on the hatchery),

- daily or twice-daily inflow of "food" made up of single-cell algae and their culture bath, which may radically change the chemical and bacteriological balance of the seawater containing the larvae.

2.4 FACILITIES AND PROCEDURES

Functional use of space is one of the factors of success of a hatchery. Not only does this prevent unnecessary fatigue (by reducing waste steps), it also makes it possible to maintain hygiene in the hatchery (for example, Hatchery 25).

Tanks and pipes are the basic elements of a hatchery, and it is essential that these be accessible for easy and rapid cleaning. They should also be easy to disassemble and transform.

In culture procedures, efforts should be directed towards simplicity and automation, although without neglecting any control measures, such as bacterial control (counting), monitoring the state of algae and larvae (by microscopic observation), algae and larvae counts, monitoring larval growth.

3. STRATEGIES WITH RESPECT TO ORGANISMS

3.1 LARVAL ECOPHYSIOLOGY

The following summaries may be consulted: LUCAS 1982b (78 references), BAYNE 1983 (149 references), LUCAS 1984 (79 references).

Larva feeding is the key to success, but this depends on intrinsic influences (quality of oocytes at spawning) and extrinsic influences (quality and quantity of particulate food).

It might be noted that most hatcheries use similar mixtures, from the same algae stocks, depending on the age of larvae: this almost universal practice seems to indicate that the method used is effective. The same is true of rearing temperatures, which depend on species.

It is nevertheless the case that mortality (in particular sudden and extensive mortality) remains frequent and represents the main cause for hatchery failures.

This mortality may be due to metabolic, toxic or pathological causes, but in most cases hatcheries discard defective cultures without seeking to determine their nature or even to keep samples for further examination. This is why there are so few studies and so little knowledge about this aspect.

Metabolic causes may be detected by observing the larvae eplifluorescently (to determine intensity of ingestion and speed of digestion) and by looking for indications of conditions such as MO/MI or fat content (using the simple method of staining with Soudan black). Information may also be obtained through post-mortem histological studies.

Toxic causes are of external origin: a substance (or the synergic effect of several substances) causes poisoning of the larvae. Normally, we think here of algal metabolites and especially of bacteria present in cultures, but here again, our knowledge is very scant.

With respect to pathological causes, the influence of vibrios has now been demonstrated (LEIBOVITZ, 1978; BROWN and LOSEE, 1978; JEFFRIES, 1982; BROWN, 1983; BROWN and ROLAND, 1984) to be due to toxins spreading through the environment rather than a direct influence of an infectious nature, which brings us back to the previous case.

3.2 ECOPHYSIOLOGY OF METAMORPHOSIS

Larvae able to metamorphose, or competent larvae, have morphological characteristics (presence of an "eye", appearance of a very mobile foot, etc.) which are well known to hatchery operators, and biochemical characteristics on which biologists are far from being in agreement. It is generally accepted that competent larvae should contain a certain proportion of fat reserves. These may be measured by colorimetry or by microchemical analysis, but in actual fact accurate information on this subject is lacking at the present time.

In addition to the classic ecological factors (temperature, light, nature of substratum, etc.), research on the start of metamorphosis in competent larvae is currently proceeding in two directions: isolation of favourable strains of bacteria, some of which are melanic, and isolation of biochemical substances such as gaba or cyclohexadienone.

If powerful means of starting metamorphosis were found, it could be used in hatcheries to synchronize the phenomenon, which would save time and make for easier management.

3.3 INFLUENCE OF SPECIES

In bivalve hatcheries, methods are designed for the general case, which is that of oviparous and gonochoric species (Japanese oysters, various clams, pectinids, mussels, etc.).

Procedures must be modified for special cases:

- larviparous species (e.g. flat oysters) in which the female incubates the young larvae in her mantle cavity for 8-10 days,

- hermaphrodites (e.g. scallops), in which the combining of male and female gametes of a given individual may lead to self-fertilization. This phenomenon is held to be detrimental to the future development of the product, and efforts should be made to prevent it.

Some species are easier to cultivate than others. The mussel *Mytilus edulis* and the small American species *Mulinia lateralis* are reputed to be easy to rear, and they are accordingly used as experimental species. Conversely, pectinids are difficult to rear, in particular *Pecten maximus*, which it has so far not been possible to produce industrially. Between these two extremes lie the common hatchery species: flat and Japanese oysters and various edible clams.

CONCLUSION

This attempt to elaborate a hatchery development strategy (without reference to economic considerations) has brought to light the complexity of the biological problems involved in this activity.

Most operating hatcheries use varying biotechnical methods, of a mainly empirical nature. The result is that, technically, it is difficult to draw an overall picture. Certain techniques, such as the culture of algae for larval feed, are nevertheless better understood than others, and are thus fairly constant from one hatchery to another.

Conversely, knowledge of seawater quality (in which the larvae move, feed, breath, excrete and defecate) and of larval ecophysiology (organisms in constant evolution, changing from pelagic to benthic with metamorphosis) is far from satisfactory. Progress with respect to these two problems in hatcheries will be derived from progress in basic science, and it is accordingly suggested that two panel discussions, one on seawater quality before and after treatment, and the other on the ecophysiology of the larvae and postlarvae of bivalves, be organized at an international level.

HATCHERIES CITED

All the hatcheries cited are followed by a date, given the fact that hatchery technology evolves considerably over time, and also that some of these hatcheries are now closed. It was not an easy task to make a complete survey of closures, but where we were able to find this information, either for 1985 or previously, we have marked with an F those hatcheries that were closed and with an A those which, to our knowledge, were active in 1985.

Hatcheries are listed by chronological order of studies (personal visits, examination of documents, or both).

REFERENCE NO.	STUDY DATE	ADDRESS	PRODUCTION	DATE OPENED
01	5/66	(F) Vanderborgh Co. Oyster Bay, Long Island, N.Y. U.S.A.	*C. virginica*	1964
02	2/69	(F) "La Hatcherie" Le Faou - Finistère FRANCE	*O. edulis*	1968
03	7/69	(F) Pacific Mariculture Inc. Pigeon Point Pescadero CA 94060 U.S.A.	*C. virginica* *C. gigas* *O. edulis*	1964

04	4/74 3/77 5/81	(A) SATMAR. Société Atlantique de Mariculture. La Saline. Gatteville-Phare 50760 Barfleur FRANCE	*O. edulis* *C. gigas* *T. philippinarum* *P. maximus*	1972
05	5/74	(F) Unicorma. Ile d'Houat Morbihan 56170 FRANCE	*C. gigas*	1974
06	5/74	(F) Générale d'aquaculture 56720 Plouharnel FRANCE	*C. gigas*	1973
07	7/74	Oyster Research Laboratory. Matoya Mie-Ken JAPON	*P. martensii* *C. gigas*	
08	5/75	(A) Flowers Co. Bayville Long Island, N.Y. U.S.A.	*C. virginica*	1962
09	5/75	(A) Blue Points Co. Sayville, Long Island N.Y. U.S.A.	*C. virginica* *M. Mercenaria*	1920
10	5/75	Long Island Oyster Farms Inc. Northport Harbor N.Y. U.S.A.	*C. virginica* *M. Mercenaria*	1971
11	5/75	(F) Chesapeake Sea Farms Inc. Ridge Maryland U.S.A.	*C. virginica*	1975
12	5/75	(A) VIMS Eastern Shore Laboratory Wachapreague Virginia U.S.A.	*M. mercenaria* *A. irradians*	1969
13	5/75 12/79	(F) International Shellfish Enterprises Inc. Moss Landing California 950.39 U.S.A.	*O. edulis* *C. gigas*	1970
14	5/75	(F) Pigeon Point Research Center. Pigeon Point Pescadero CA 94060 (succeeded 03) U.S.A.	*C. gigas*	1974
15	5/75	(F) Lummi Indian Project Bellingham Washington U.S.A.	*C. gigas*	1972
16	5/75	(F) Sea Farms Inc. Poulsbo Washington 98370 U.S.A.	*C. gigas*	1973

17	5/75 9/82	Seasalter Shellfish Ltd. The Harbour. Whistable. Kent G.B.	*M. mercenaria* *C. gigas* *O. edulis* *T. decussatus*	1972
18	11/78	(A) Aquamaré, Route Diette 17590 Ars en Ré (now SICAMAIR) FRANCE	*C. gigas*	1977
19	9/81	(F) Industrial marisquera Villajuan. Villagarcia (Pontevedra) Galicia Spain	*C. gigas* *O. edulis*	1981
20	9/81	Planta de cultivos marinos Muelle de Porcillan. Ribadeo (Lugo) Galicia. Spain	*T. decussatus* *O. edulis*	1978
21	5/82	Intertide Corporation North Hapswell Maine 04079. U.S.A.	*O. edulis* *M. mercenaria*	1980
22	5/82	(F) Cozy Harbour Sea Farms Pratt is Island Road. West Southport. Maine. 04576 U.S.A.	*O. edulis* *M. mercenaria*	1979
23	5/82	Marine Bio Service. High Island South Bristol Maine. U.S.A.	*O. edulis* *C. virginica* *M. mercenaria*	1981
24	5/82	(F) Bristol Shellfish Farms. Round Pond. Maine. 04564 U.S.A.	*O. edulis* *C. virginica* *M. mercenaria*	1980
25	6/82	(A) Whiskey Creek Oyster Farm. Bayshore road Tillamook. Oregon. 97141 U.S.A.	*C. gigas*	1977
27	6/82	(A) Experimental Hatchery Manchester. School of Fisheries. University of Washington Seattle U.S.A.	*C. gigas*	1974
28	6/82	Boet-mor/Sea Food. Cus-Hastraugh Claddaghduff Co.Galway. Irlande	*O. edulis* *C. gigas*	1980
29	6/84	(A) IFREMER. Les viviers d'Argenton. 29236 Landunvez. France	*P. maximus*	1983
30	6/84	(A) Ecloserie.Nurserie Le Tinduff. 29213 Plougastel-Daoulas. France	*P. maximus*	1983

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INNOVATIONS IN THE NURSERY CULTURE AND MATURATION OF BIVALVES

J.P. FLASSCH *

ABSTRACT

Innovations in the nursery culture and maturation of bivalves are being worked on at all levels of research and production, but transfer to the development stage must be effected differently in each case. Over the past twenty years, there have been a great many innovations in bivalve rearing, most of which may be described in terms of rearing conditions: higher and lower densities; confined or open environemnt; overflow; upwelling; floating, suspended, raised or ground systems, etc. The quality of an innovation is characterized by its influence on the efficient operation of the specific culture program and by how easily it may be transferred.

key words: innovations, molluscs, bivalves, nursery culture, maturation

RESUME.

Les innovations en matière de prégrossissement et de grossissement de bivalves sont mises au point à tous les niveaux de recherche et de production; selon les cas, le transfert au développement devra s'effectuer de façon différente. Depuis ces vingt dernières années, l'élevage de bivalves a profité de très nombreuses innovations dont les principales sont décrites en fonction des conditions d'élevage à haute et plus faible densité, en milieux confinés, en milieux ouverts , (l'"overflow", l'"upflow", les systèmes flottant, suspendu, surélevé, en sol, etc.) La qualité d'une innovation est caractérisée par son influence sur le bon déroulement de l'élevage considéré et sa capacité à être transférée.

mots clés : innovations , mollusques , bivalves, prégrossissement, grossissement.

* IFREMER, Centre de Brest, Laboratoire, "Diversification de la Conchyliculture" (Shellfish Industry Diversification), B.P. 337, 29273 **Brest** Cedex, France

INTRODUCTION

Any innovation should be characterized by its simplicity of implementation and application, and should permit the best possible use of the optimum conditions offered by various natural environments.

New techniques that improve production are quite often also dependent on the climate, geography and, above all, the socioeconomic conditions of the countries where they are implemented, and are thus not always directly application to other countries than that where they originated.

Another observation may be made: in high-yield basins, innovations are rare. Pressure on the part of operators and the routine nature of the work very often run counter to the propagation of new ideas and their application, while in new or low-yield basins, the innovative spirit is much more likely to manifest itself.

Over the past fifteen years, use of plastics has been one of the determining factors in the initiation of new techniques. As well, control of bivalve spat production following work by Loosanoff and Davis (1963) and Walne (1974) has made for considerable progress in nursery culture and even maturation techniques.

I - NURSERY CULTURE, A TRANSITION STAGE

This phase extends from metamorphosis to the intermediate size, from which the bivalve will then be raised at densities close to that necessary to obtain market size. This question was dealt with extensively at the Ghent conference (Nursery Culturing of Bivalve Molluscs, 1981).

The various advanced techniques used depend on the size of spat and rearing density, and may be described as follows:

1 - HIGH DENSITY NURSERY CULTURE

Rearing density: 10^6 to 5.10^4 individuals/m^2

1.1 Hatchery

Metamorphosed spat is matured in the hatchery to a size of approximately 2 mm. This phase requires the addition of food and thus controlled production of single-cell algae. The phytoplankton is transported with the distribution of seawater, and temperature is strictly controlled.

Two techniques are commonly used, depending on the age of spat and the species involved.

- Overflow

  The water current is made to flow downwards. This current is created either by direct inflow or by the use of an "air lift". The water circuit may be either open or closed in order to save energy.

  The rearing unit is made up of frames or cylinders measuring 0.15 m and 0.50 m in height respectively. The spat lies on a screen with a mesh size appropriate to the size of the molluscs being reared. In both cases, the area of the screen is in the order of 0.2 m. Holding tanks are normally made of polyester.

  This technique is used for the three major families of bivalve molluscs *(Ostreidae, Pectinidae* and *Veneridae)*.

- Upwelling

  The water current is made to circulate upwards by "air lift" or using a gravity system. The rearing enclosure is formed by the cylindrical screen. This technique is used for all species with the exception of pectinids.

These two systems are used in both the United States and Europe, with rearing densities in the order of $10^6/m^2$.

1.2 Land bases

Rearing temperature is that of seawater, and food flows in naturally. Rearing densities range from 5.10 to $0,5.10/m^2$.

The gravity effect may be obtained by pumping (Bayes, Claus and Leborgne, 1981) or by an engineering arrangement (Bouin* station in France). Where pumping is used, the two techniques used are identical with the above, overflow and upwelling. The rearing enclosures in most cases are screen cylinders 0.5 m high and 0.2 m in diameter. Receiving tanks are concrete or polyester.

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*IFREMER Station, Bouin Basin oyster-culture zone.

- Overflow

This system is mainly used for pectinids up to sizes of approximately 10 mm. Cylinder flow is 0.7 m^3/h, and rearing densities vary between 5.10^5 and $0,5.10^5/m^2$. There has been considerable development in the nursery culture of scallops in France at the Le Tinduff farm*).

- Upwelling

Application of this technique is made possible using the hydrodynamic arrangement of reclaimed lands (polders) in Holland and France.

This type of unit may be installed in oyster-rearing basins using the gravity system at moderate capital costs and with no energy costs, as in the polder areas of Holland (e.g. the Ooterschelde) or the Bouin oyster-culture zone in France.

Upwelling is mainly used for nursery culture of *Ostreidae* and *Veneridae*. A very advanced technique using this method is currently under development. This involves drilling operations to use confined groundwater at constant temperatures to heat seawater through a heat exchanger. These waters, if their salinity permits, may also be used directly as a rearing milieu for the production of single-cell algae. This technique was developed chiefly for winter use, for nursery culture of spat. Given the cost of the operation, it now remains to prove that spat red during the winter show better growth potential in the spring than spat raised in the fall using conventional techniques.

This technology was developed in hatcheries in the United States and in France at the SICAMAIR hatchery and in the IFREMER experimental station at Bouin, for use in nursery culturing.

The rearing density that produces the best growth performance varies with size, from 1,25 to $0,5.10^5/m^2$, and the flow per screen cylinder is 3 m^3/h.

This nursery culturing method is mainly being used in the United States and Europe.

2 - LOW DENSITY NURSERY CULTURING

Rearing densities: 3.10^4 to $0,2.10^4/m^2$. Water flow is not forced and food is supplied naturally. This method makes the best use of the outside environment potential.

Nursery culturing may be done out of the ground, on ground or underground.

2.1 Out of ground

- Floating system

The rearing structure is normally made up of a wooden frame 0.03 to 0.10 m high equipped with a screen of appropriate size. The enclo-

*Station working with IFREMER and managed by the local maritime fisheries committee of Brest. The activity is part of the pluriannual scallop program for which spat is produced for recolonization purposes.

sure is made up of two frames placed one on top of the other, with the upper frame being inverted (this technique is extensively used by the AGCM*).

Densities vary from 3.10^4 to $5.10^3/m^2$ for venerids and $3.10^3/m^2$ for pectinids. In the case of scallop spat, the screen in the upper part of the enclosure is replaced by a sheet of black plastic (a technique developed by the SATMAR**).

This type of nursery culture is practised on the coasts of France as well as in marshes in Senegal.

- Suspended system

This technique, which has been used extensively in the Pacific for many years, has become more popular since the availability of nylon and other plastics. A number of innovations have been developed, mainly in Japan (Davy et al., 1982; Ventilla, 1982; Ventilla, 1984).

Nursery culture on strings is practised on *Ostreidae* spat collectors for Japanese oysters or inside collectors for the scallop *Pactinopecten yessoensis* (Ventilla, 1982). Early maturing may be continued in cages or baskets (Pacific scallops and mussels).

The string structure may be replaced by rafts (oysters and mussels in Japan and Portugal, and clams in France).

- Raised system

The technique of rearing on above-ground structures has developed considerably over the past few years with, for instance, the tripod for nursery culture of pearl oysters in the Pacific, the oyster-culture table developed in France in the deep waters of Brest Harbour for early maturing of scallops from 3 mm up to 30 mm (3-15 mm in baskets at $9,000/m^2$, 15-30 mm in cages at $1,000/m^2$). The oyster-culture table commonly used in open areas holds cultch (Japanese oysters) or plastic mesh bags (hatchery spat). The plastic collection tube permits nursery culturing up to 12 months or even 18 months at the latest. For venerids, the structure developed for the floating system is also used on oyster-culture tables. If cleanliness standards are observed, this type of nursery culture may be practised without stress at densities of 3.10^4 to $10^4/m^2$.

2.2 On-ground and underground

This method basically applied to nursery culture of venerids, from spat up to 3 mm.

The spat may be placed in 0.1 m plastic mesh bags of a new type. These bags are placed right on the ground. This technique makes it possible to use protected areas (ponds, claires, marshes). Nursery culture may also be carried out between two layers of netting, either on the foreshore or in protected areas. Size after early maturing varies and may be up to 25 mm (5 g). Optimum rearing density is $2\ 10^3/m^2$.

*Association Guérandaise de Cultures Marines, France (Guérande aquaculture assoc.)
** Société Atlantique de Mariculture, France.

Nursery culture is an indispensable stage which, depending on the culture techniques used, will have major repercussions on the animal's later life.

II - MATURATION

Maturing takes place in the last stage of the animal's life, up to the time it reaches marketable size. During this phase density may vary, but should not change by any more than a factor of 2.

In many cases, the techniques used are comparable to those used for preculturing.

1 - OUT OF GROUND

1.1 Suspended rearing

- Strings and rafts

These two systems, although of different structure, generally use the same rearing units and are based on the biological advantage of reáring right in the water.

In the Pacific, and particularly in Japan, these technical and bio-technical innovations (Ventilla, 1982) have been responsible for a major increase over the past fifteen years in production of cultured scallops, which rose from 10,000 tonnes in 1971 to 60,000 in 1981 (official statistics from the Japanese fisheries authorities).

The same is true for the pearl oyster *(Pinctada fucata)*, where pearl production was kept stable (42 T in 1981) through application of new techniques to these species, with aquaculture completely replacing harvesting of wild oysters.

Mussels have also been farmed extensively on rafts, both in the Pacific (India, Japan) (Davy, F.B. et al., 1982), and on the Atlantic coast (Spain and Portugal).

Suspended rearing from frames fixed in the ground has developed considerably in areas with low tidal amplitudes for farming of flat oysters and mussels (Etangs Méditerranéens farms in France). The shellfish are attached with cement or polyster glue on bars or strings hanging vertically down from frames.

1.2 Raised culture

A major part of French oyster production comes from rearing on tables using plastic bags. This innovation permits standardization of culture (better manpower organization, better control over biological parameters) provided norms are respected for culture densities, management of structures, etc.

The seed placed in the bags may be of natural origin, once it has been removed from cultch, or come from hatcheries. In this connection, a new phenomenon has been observed in France: the use by certain professionals of hatchery product alone, even where natural supplies are available. For the past four years, the SATMAR company has been supplying

four oyster farmers in Brittany and Normandy with 26×10^6 spat separated from one another by 6-8 mm. The spat is placed in mesh bags at the beginning of the year at densities of 500/bag, or 1500/m^2. At the end of the year, average weight is approximately 30 g, or 13 kg/bag. The animals are then planted right in the ground and reach a weight of 60 g by the end of the following year. Survival is in the order of 85%, and annual tonnage is 1,300 tonnes. In this case, natural growth potential is perfectly duplicated, and the growth curve for cultured oysters is quite close to the optimum natural curve while respecting the profitability standards of the operation.

2 - UNDERGROUND

This technique is used for commercial species of *Veneridae*, such as hard clams in the United States and cockles and hard clams in the Pacific and in Europe.

It is in the United States, for hard clams, and especially in France, for carpet-shells, that the techniques under development are most strongly inspired by marshland cultural practices.

The basic obstacle to this type of culture is the problem of predators, with the main predators being crabs and, in some cases, fish.

Protective measures tailored to the habits of the main predators involved are of two types: horizontal protection and vertical protection.

2.1 Horizontal protection

In this type, the facility may be covered by a grill or a layer of netting. The main problem with this method is the difficulty of precise monitoring, since access to the culture is particularly difficult.

Two adaptations have been applied to the rearing of the clam *(Ruditapes philippinarum)*: rearing in buried cages or under nets.

The cage has a grill on its lower side, which is filled with sediment and then covered with a screen once the seed is in place. The surface is 0.3 m, density is 700/m^2, and the rearing cycle is from 24 to 28 months. The cages are tied into strings that may be raised at high tide. Harvesting in this case is greatly simplified. The structures are lifted onto the deck of the boat and then washed with a hose. The openings in the grill on the underside allow the sediment to flow out and hold the clams in. This technique, although somewhat cumbersome, is used in France by several clam-farmers (France, Gulf of Morbihan, 10 to 12 T/year).

Rearing under nets, which has been experimented in the United States in Puget Sound on *Ruditapes philippinarum* (Anderson et al., 1982) has not yet produced significant amounts of product. In France, this technique is spreading, but is still in the development stages. It offers the advantage, on hard ground, of allowing the use of machines for planting and installing nets. The main interest of this method is that it offers no resistance to bad weather and currents. A negative net effect has nevertheless been observed on growth, due to the inevitable silting over of surfaces even with intensive brushing operations. Weights of 20 g are reached in 26 months.

2.2 Vertical protection

This technique, which is more difficult to implement in areas that are exposed and have very strong currents, nevertheless has the advantage of not placing any stress on the crop which, provided optimum densities are respected, develops naturally in enclosures where access and monitoring are extremely simple.

The enclosure method was developed in the United States on the Virginia coast (Castagna and Craeuter, 1981) for hard clams. Since tidal amplitude is fairly slight in this region (3 m), the enclosure in this case is high enough to prevent entry by a swimming crab, the blue crab *Callinectes sapidus*, and the eagle ray *Rhinoptera binasus*. The effectiveness of this protection is increased by adding fine gravel (Kraeuter and Castagna, 1980).

This technique is being developed intensively, mainly on the Atlantic coast of France in the intertidal zone, between 2 and 2.50 m above hydrographic zero, for culture of the clam *R. Philippinarum*. Here, the main predator is the green crab *Carcinus maenas*, which is a climber rather than a swimmer. Culture is carried out in enclosures. The effectiveness of the barrier (45 to 50 cm) is increased by attaching to it a plastic element (plastic sheeting folded over into a teardrop shape) which, when well maintained, is certain to prevent the predator from getting through. Protection effectiveness is also increased by adding fine gravel, which limits predation when young crabs develop inside the structure. This additional protection is also effective against attack by fish (bream and flatfish).

If the maturation period at the beginning of the year is respected, the culture cycle is 20 months (for an average weight of 20 g) for rearing densities of 250 clams/m^2.

CONCLUSION

This list of innovations in the field of preculturing and culturing of bivalve molluscs is not exhaustive, since there exist a great many variants of these methods.

We have not mentioned scientific and technical research that has not led to any applications for technical or economic reasons.

An innovation may thus be one element of a given research or production activity, or it may itself constitute the whole research project.

Depending on the case, transfer of this innovation will be carried out in various ways. For example, the upflow technique, used in nurseries and described in great detail in reports and other publications, may be put into application quite rapidly by producers. Conversely, an innovative culture method such as that of *P. yessoensis* in Japan or *R. philippinarum* in France cannot be transferred using the same methods, since these types of culture are broken down into small stages which, while simple and original, are occasionally still evolving, thus making it both difficult and dangerous to use publications or manuals that have been written up too hastily. In such cases, research should accompany the innovation, insofar as possible, up to the point where a definite culture procedure is developed. This participation of research in development work should be done very cautiously and evaluated according to the individual case and species.

Any innovation, however, if it is to be usable, must not be too disturbing to the biological results; it should make the best possible use of natural growth potential. As well, experiments should not be confined to unnecessarily short periods in the bivalve life cycle.

A decline in biological yields, that is, a flattening of the growth curve and mortality, may occur for three main causes:

1) negative effect of the technique on the harmonious development of the species involved,
2) deterioration of the environment,
3) degeneration of the population being reared.

In most cases, the first cause is, in the short or long term, the trigger for the other two. Deterioration of product quality is then very rapidly observed, as is the increasing frequency of diseases capable of destroying the entire crop in a very short time.

It is therefore wise to devote some preliminary work to standardizing biotechniques as development progresses, rather than trying to solve problems after the fact, since at that point in time, the measures that must be taken are liable to be extremely costly.

This is why it is essential to establish simple zootechnical references, in close cooperation with the professionals involved. These could include "pilot curves" on an international scale for species being raised in different geographic areas, and then on a national level for each site and for the various techniques used. Operators must be able to compare their own observations to standards which they can easily obtain from local sources (co-op headquarters, regional offices, etc.).

It might also be proposed that studies be carried out, for several reference species, on the effect of nursery culturing techniques on eventual growth in order that spat quality categories may be developed. To do this, it would be well to have reference curves prepared in advance that could be adapted to take into account individual and annual variations. This would presuppose standardized techniques and very close communication among laboratories in the various countries involved.

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MANAGEMENT OF SHELLFISH CULTURE ECOSYSTEMS

GESTION DES ECOSYSTEMES CONCHYLICOLES

SUMMARY OF MANAGEMENT OF SHELLFISH CULTURE ECOSYSTEMS

P. BELAND *

ABSTRACT

The history of mollusc culture in natural habitats in France and Japan shows that intensive cultures must be adjusted to the carrying capacity of the ecosystem.

Oyster culture in France suggests that overstocking drives the system towards an unstable state, which is expressed in terms of irregular growth, increased time to marketable size, increased mortality and incidences of disease. In such a context of high densities and physiological stress, epizooties can eliminate whole cultures. In Japan, it has been recognized that scallop cultures must be adjusted to limit below carrying capacity. Natural productivity as measured by minimal phytoplankton production, growth curves and required size for marketing are integrated into resource management procedures.

A number of factors determine the maximum density for a culture where that goal is to stabilize production within given limits. These factors are linked to the biological characteristics of the cultured and other associated species within the ecosystem, to the culture system itself, to the hydrographic and production patterns of the basin, to climate and to human interventions. It is important to take into account the natural variability of such factors as well as their potentially synergistic interaction. In particular we recognize the importance of the following dynamic processes :

- The interraction between the culture system, currents and sedimentation. It may lead to shoaling with a corresponding decrease in the availability of food and quality of water. The culture also contributes to deleterious changes in the substrate and adjacent water through the accumulation of organic matter ;

- The induction of competitive and/or predatory interaction from species whose presence and numbers are facilitated by the culture ;

- Variations in the supply of nutrients that promote the natural productivity of a basin ;

- The incidence of contaminants affecting either the cultured molluscs at any stage of their life cycle or the quality and quantity of their food, pathogens and competitors.

Any variation in one or the other of these factors will lead to a progressive and possibly permanent, readjustement of the biomass and expected production (growth, reproduction) that the natural system can support.

In addition to empirical knowledge derived from the observation of cultured populations we recognize the value of an analytical approach based on an understanding of mechanisms acting on populations as part of a system. As a

* Fisheries Ecology Research Center, 310 avenue Les Urselines, **Rimouski**, Québec, G5L 3A1, Canada

first step, we need trophic models that include the movements of water masses, the factors controlling the production and availability of natural food, the energy budget corresponding to the age structure of the cultured animals. Ultimately, there is a need for more comprenhensive models that include an evaluation of gains and losses that are attributable to variations in water quality, pathogens, competitors and predators. It is important that development in the fields of aquaculture technology and genetics be attuned to the requirements for survival, growth and production in the natural basins where are molluscs farms.

Coastal areas that are suitable for mollusc aquaculture are in demand for other human activities that are potentially conflicting. In this context, predictive and reliable ecological models describing mollusc yield from a system are an essential tool to the decision-making process. To evaluate the impact on economy and employment of aquaculture operations, managers need to know what levels of production can be expected from biological systems under various loads. Without considering the overall changes induced in natural systems by aquaculture operations, the long term benefit to society cannot be assessed properly.

RÉSUMÉ DE LA SESSION SUR LA GESTION DES ÉCOSYSTEMES CONCHYLICOLES

P. BELAND *

RESUME

L'histoire de la conchyliculture en France et au Japon montre que les cultures intensives doivent être adaptées à la charge utile de l'écosystème.

L'exemple de l'ostréiculture en France conduit à penser que la surpopulation entraîne une instabilité de la production, traduite par un déficit de croissance, provoque un accroissement du temps de rotation des stocks et une augmentation des mortalités et accroît les risques de maladies. Dans un contexte de surpopulation et de stress physiologiques les épizooties peuvent décimer des cultures saines. Au Japon, il a été mis en évidence que le stock cultivé de coquille St-Jacques doit être en dessous de la charge utile. Les modèles d'exploitations des ressources intègrent la productivité naturelle, mesurée par la production minimale de phytoplancton, les courbes de croissance et la taille minimale de commercialisation.

La stabilisation d'une production, dans des limites données, dépend de plusieurs facteurs qui déterminent la densité maximale. Ces facteurs sont liés aux caractéristiques biologiques des espèces cultivées, aux espèces compétitrices, aux méthodes d'élevage, à l'hydrographie, aux types de production du bassin, au climat et aux interventions humaines. Il est important de tenir compte de la variabilité normale de tels facteurs ainsi que de leur synergie et interactions potentielles. Nous reconnaissons, en particulier, l'importance des processus dynamiques suivants:

- l'interaction entre le système de culture, les courants et la sédimentation. Elle peut conduire à une diminution de la production, conjointement à celle de la qualité de l'eau et de la nourriture disponible. Les cultures contribuent également à la détérioration du substrat et de l'eau du fait de l'accumulation des matières organiques.

- l'introduction de compétiteurs et/ou de prédateurs, dont les cultures augmentent le risque de présence et le nombre.

- les variations des apports de nutriments qui favorisent la productivité naturelle d'un bassin.

- l'incidence de polluants qui affectent, soit les mollusques à tous les stades de leur développement, soit la qualité et la quantité de nourriture, ou qui peuvent favoriser les pathogènes et les compétiteurs.

N'importe quelle variation de l'un ou l'autre de ces facteurs conduira à un réajustement progressif de la biomasse et de la production attendue (croissance, reproduction) compatible avec la capacité de l'écosystème.

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* Fisheries Ecology Research Center, 310 avenue Les Urselines, **Rimouski**, Québec, G5L 3A1, Canada

En plus des connaissances empiriques, provenant de l'observation des populations élevées, nous reconnaissons la valeur d'une approche analytique fondée sur la connaissance des mécanismes régissant les populations en tant qu'élément du système. En première approche nous avons besoin de modèles trophiques incluant les mouvements des masses d'eau, les facteurs contrôlant la production et la disponibilité de la nourriture, et les besoins énergétiques par classe d'âge.

In Fine, des modèles plus précis sont nécessaires pour évaluer les gains et les pertes liées aux variations de qualité du milieu, aux agents pathogènes, aux compétiteurs et prédateurs. Il est important d'harmoniser le développement de la génétique et des technologies nouvelles, avec les conditions requises pour obtenir une survie, une croissance et une production dans les bassins conchylicoles.

L'espace littoral favorable à la conchyliculture est sujet à des demandes pour d'autres activités, et il se crée une situation conflictuelle. Dans ce contexte, des modèles écologiques prédictifs fiables, décrivant la production de mollusques dans un système, sont des outils essentiels à la prise des décisions. Pour évaluer l'impact de l'aquaculture sur l'économie et sur l'emploi, les responsables ont besoin de connaître le niveau de production susceptible d'être atteint dans des systèmes biologiques soumis à des variations. L'avantage, à long terme, pour la société ne peuvent être évalués correctement sans prendre en compte les changements induits sur l'écosystème par l'aquaculture.

BIVALVES AND ENVIRONMENTAL CONTAMINANTS

A. RENZONI *

Abstract : bivalve molluscs are under the threats of contaminants ; also as they concentrate them they can transmit to predators, with increased effects, especially to humans. Effects of main chemical pollutants (oil products, metals, organochlorids) are revised. Differences among species are frequently wide. Using bivalve molluscs as pollution indicators has shown limited interest for practical means, after a long and extensive study. But these works had other important consequences. Even with all the informations collected on contaminants and their process in the tissues and the ecosystems, there are still numerous questions about their cycles, synergies and the ways of evaluating effects of contaminants on living organisms. National and international lawmakers need answers to these.

Résumé : Les mollusques bivalves subissent les effets des polluants mais aussi en accumulant ceux-ci peuvent les transmettre en les amplifiant a leurs prédateurs, notamment à l'homme. Les modes d'action des principaux polluants chimiques (produits pétroliers, métaux, organochlorés) sont présentés. Les différences entre espèces sont souvent importantes. L'intérêt des bivalves comme indicateurs de pollution s'est révélée, après des travaux systématiques importants, assez limitée dans la pratique ; mais ces travaux ont eu des retombées importants. Malgré la somme de connaissances accumulées sur les polluants et leur devenir dans les organismes et l'écosystème, de nombreuses questions restent sur leur cycle, leurs synergies, les méthodes d'évaluation de leurs effets sur les organismes. Les réponses sont nécessaires pour les législateurs nationaux et internationaux.

* Department of Environmental Biology, University of **Siena**, Italy

INTRODUCTION

The aim of this section is to evaluate the impact of anthropogenic pollution on organisms included among the so-called shellfish. Actually this would and should include crustaceans, but molluscs are our subject here; mostly because aquaculture production and related economic interests are, at least in Europe, much greater for molluscs than for crustaceans.

1- BACKGROUND INFORMATION

During the last 100 years the enormous increase of industrial activity, as a consequence of the explosion of the human population, has been accompanied by the destruction of several bivalve grounds; in some cases the domestic and industrial sewage has contributed to the phenomenon only slightly, in other cases it is the main cause. Before this century most coastal waters were in good condition and prerequisite of sea water of good quality was fulfilled both for the natural production of fish and shellfish and for aquaculture. Water quality has been deteriorating progressively until recently; now however (even though man has devoted his attention more to the economic and energetic crises) the situation seems to be slightly improving.

Pollution as it affects shellfish constitutes a double threat: the first is to the shellfish themselves due to the high levels of xenobiotics present in the water affecting various metabolic activities (respiration, enzyme production, larval life, etc.) and therefore reproductive success; the second is to humans eating these filter-feeders, which concentrate chemicals in their tissues.

Some species of bivalves (in particular various species of oysters) are very sensitive to pollutants. The impact of the great industrial

activity and the consequent increase of the pollution of various coastal areas can be summarized by a frequently reported example: in New York State, well known for its oyster production, from 1920 to 1970 the production of oysters declined by 99%; domestic and industrial pollution as well as virus, bacterial and protozoan diseases (beacause of the reduced defence capacities of the bivalves) have been considered responsible of the virtual disappearance of those organisms.

However pollution is not the only cause of the sharp reduction in marine production. During the last century marine and fresh-water "fish" resources have been exploited greatly and in some areas there is evidence that because of an over-exploitation some valuable benthic stocks (fish, molluscs and crustaceans) have almost disappeared. For this reason (and for the economical advantages) much effort has been dedicated to aquaculture during recent decades. Among the organisms suitable for a rewarding aquaculture, besides plants and fish, crustaceans and molluscs are cultivated in many countries, in bays, harbors, lagoons and artificial coastal ponds.

Bivalves have been cultivated through the ages; in fact oysters were cultivated during Roman times. Most of the bivalve production still derives from natural stocks on intertidal or sub-tidal beds harvested by professional fishermen; some species (oysters and mussels) are mostly cultivated; both groups are very important as food for human consumption.

During the last decades, the request for animal proteins has greatly increased and aquaculture has been able to meet some of this demand. To give an example, the figures for oyster and mussel production from natural stocks and aquaculture, as reported by F.A.O. for 1982 are MT 955900 and 637863 respectively. Every year a greater proportion derives from aquaculture and reports predict a world aggregate (natural and aquaculture) production for oysters of 2,450,000 MT roundweight by the year 2000.

In a period of energy crisis edible molluscs are one of the best organisms to cultivate since they are the most efficient converters of the organic matter produced by phytoplankton (the first link of the food

chain) into human food. In addition to this, their broad distribution and the possibility of their cultivation in coastal waters is of enormous advantage: for fishermen and/or aquaculturists. On the other hand coastal waters are much more susceptible than pelagic open sea waters to natural contamination and anthropogenic pollution.

Independently of the species considered, for most animals the larval period is incontestably the most sensitive to chemical and physical variations of the sorrounding environment. Thus in addition to general efforts to reduce pollution in areas suitable to bivalve cultivation more hatcheries have been set up and, in some countries, facilities for rearing juveniles have also been built (inland as well as along the shores).

Clam, scallop and oyster hatcheries are working commercially at a profit in U.S.A., Japan, Great Britain and France.

Of the pollutants eliminated by man into the atmosphere and terrestrial and marine environments, we will confine our attention to oils and dispersants, heavy metals and chlorinated hydrocarbons.

2- CONTAMINANTS: LEVELS AND EFFECTS

2.1 Oil and dispersants

Before entering into details regarding the toxicity of these pollutants I would like to remind you that most of the information available so far is related to sub-lethal concentrations rather than to the lethal doses occuring during an ocean accident or obtained experimentally in the laboratory. Even though we will deal mostly with the effects of sub-lethal concentrations, we consider it worthwhile to give some information regarding the toxicity of high levels of these hydrocarbons.

Research on bivalves indicates that when specimens are kept in water with such substances they are accumulated in the lipid pools (Stegeman

and Teal 1973). Lee et al. 1972, after observing that mussels accumulate greater quantities of paraffinic hydrocarbons than aromatic compounds, found that the hepatopancreas is the site of the hydrocarbons storage and that on transfer to clean sea-water, they were able to eliminate almost all the hydrocarbons accumulated for Crassostrea virginica (Stegeman and Teal 1973) and for Mytilus galloprovincialis (Fossato e Siviero 1974).

Regarding sensitivity to oil there is a great deal of difference from one bivalve species to another. According to Hawkes (1961) the quahog Mercenaria mercenaria seems to be "practically immune to oil pollution..... ....in Narragansett Bay (Rhode Island) where the bottom is literally paved with oil". Instead, stocks of pisa clams (Tivela stultorum, Hampson and Sander 1969) and razor clams (Siliqua pratula, Telberger 1964) suffered heavy mortalities when polluted by fuel-oil spills or by a mixture of similar oils. A similar sensitivity to dissolved oil with or without detergents has been experimentally confirmed by Nelson-Smith , and by other authors quoted by him (Leenhart 1925, Galtsoff et al. 1935, Chipman and Galtsoff 1949, Lunz 1950) who have studied the various effects of oil in Ostrea edulis, Crassostrea angulata, Mytilus galloprovincialis and Crassostrea virginica; the various discrepancies reported may be attribu ted not only to differences in the sensitivity of the species, and in the chemical composition of the oil/or of the dispersant, but also to the possibility of the bilvalve's detecting the presence of oil and/or dispersant in the water in advance and shutting its valves.

In addition to the species-related differences in sensibility to oil and differences in the composition of oil (especially the proportion of the highly volatile components) the rate of decomposition of oil components influences the degree of their toxicity. There is evidence that the life of oil components in the sea is highly variable and depends on the environment where the spills occur, on the densities of oil- degradating bacteria, on the levels of nutrients stimulating bacterial growth and

on many other circustances.

For most species the oil floating on the surface of the sea is very toxic (Patella, Littorina) although some benthic intertidal organisms (Mytilus) seem to survive relatively well. Other toxic components of the oil do not remain on the surface of the sea, but sink to the bottom sediments, where some species (the lungworm Arenicola) are more resistant than other benthic organisms (Echinocardium, Ensis, Cerastoderma). It is almost impossible to evaluate the toxicity of the various components as they sink toward the bottom of the sea at different speeds. In fact it is during this descent that most of the bacterial degradation occurs (especially when the oil is dispersed into very small droplets by natural forces or by chemical dispersants) and many components of variable toxicity are developed.

2.2 Metals

Heavy metals, even those that are essential in trace amounts, are toxic to marine organisms at relatively low concentrations. An enormous amount of data is available on bivalves with mussels as the focus of attention during the last decades (Keckes et al. 1968, Bryan 1973, Dare and Edwards 1975, Kopfler 1974, Majori et al. 1976, Phillips 1976a, 1976b, Ayling 1977, Loove and Moore 1979, George 1980, Wilson 1983). The fields of study include the occurence and seasonal variations of a given metal; the influence mixtures of various metals at low concentrations; short and long term effects. Some induce clearcut modifications even in the short term, others which appear not to be toxic in the short term, others which appear not to be toxic in the short term, turn out to be insidious poisons in the long term as some experiments with mussels have demostrated (Schulz-Baldes 1972). One of the facts that emerges from a great many of the experiments is that the presence of certain metals (copper, zinc, cadmium, molybden, etc.) dissolved in the water determines a reduction

of the pumping rate, and thus a reduction of oxygen and food availability. Bivalves react to some metals by keeping their valves closed for long periods and periodically opening then briefly.

Even so the amount of metal ions in the water they take in (together with the reduced pumping rate) may be sufficient to alter several metabolic activities, resulting in effects such as a reduction of ciliary movements, an increase in mucus production, the rejection of food particles with the pseudofeces and a general disturbance of many other physiological functions. Being at the first link of the food-chain, these molluscs feed on very short-lived organisms, which have therefore been exposed to pollutants only briefly. Hence, it is unlikely that bivalves become highly polluted by the metals accumulated within the body of the organisms upon which they feed. On the other hand by pumping large quantities of water through the mantle cavity for filtration (food particle retention) and ventilation (oxygen uptake) they can absorb large amounts of metals (dissolved in the surrounding waters).

A long series of experiments has also been conducted to evaluate the recovery of bivalves after exposure (in the laboratory or in the field) to metals dissolved in the water. In most of the studies performed, the transfer of bivalves from water polluted by metals to clean sea water has been followed by marked increase in oxygen consumption. This increased demand is thought to be related to the restoration of proper metabolic activities of tissues that have suffered, rather than a consequence of temporary closure of the valves from the presence of metals in the water.

2.3 Chlorinated hydrocarbons

During the last 40 years there has been a steadily growing interest in this group of contaminants. Since they are synthetic substances, animals that come into contact with them have trouble degrading them. They are

characterized by their lipophilic affinity and persistence in the environment and therefore are easily accumulated in animal tissues. All living organisms absorb chlorinated hydrocarbons from the water and accumulate these substances until a balance between uptake and release is attained. The uptake occurs through the body surface and the food and this fact explains why animals living in the same region may have different chlorinated hydrocarbons concentrations in their tissues and even different spectra, although they are closely related taxonomically. The concentration factors (and bioaccumulation process) are affected by the animal's type of feeding, its way of coming into contact with chlorinated hydrocarbons dissolved in the sea water or adsorbed to suspended particles and the amount of its body surface that come into contact with contaminants.

That the first of these three variab les is the most important is shown by the fact that the highest concentrations of xenobiotics and other non regulated contaminants are found in predators.

Among the chlorinated hydrocarbons DDT and its metabolites were widespread from 1940 to 1970, but since then DDT has been banned in many countries. Data from various areas of the USA in the late sixties and early seventies show that the highest levels in Mytilus edulis were obtained in California where the use of these pesticides for agricultural purposes was intense.

The release of many other chlorinated hydrocarbons from various industrial products however continues and their concentration in coastal water organisms is still high.

Like metals, these xenobiotics in sub-lethal doses influence various metabolic activities. Most of the time the primary effect is a reduction of the condition index (Roberts 1972), decrease in shell growth (Butler 1971), reduced capacity of byssus formation in Mytilus and Chlamys (Roberts 1973) and various other metabolic disfunctions. In the case of Mercenaria mercenaria, Engle, Neat and Hilman (1972) advance the hypothesis that

most of the above mentioned metabolic disfunctions are due to an increase in glucose degradation and the consequent absence of gluconeogenesis. As mentioned above many studies show that embryos and larvae are generally less resistant to pollutants than adults. This fact is true of bivalves and has been confirmed by a large number of observations (see Renzoni 1974).

Bivalve larvae make up a significant portion of the coastal plankton and, as such, they can absorb the xenobiotics; and, as food, they in turn can pass the xenobiotics on up the food chain. Their life is short (as larvae), rarely longer than a month, so that there is slight possibility of their accumulating large quantities of pollutants even temporarily. They are mobile and their swimming activity is due to the crown of cilia developed by the embryo a few hours after fertilization. After a variable period (15-35 days) of development, the larvae undergo metamorphosis and during this period several gross morphological changes occur. During this period the larval feeding mechanism is lost and a complete new (adult) mechanism is acquired. During the 2-3 days of metamorphosis the larvae do not feed. The passage from a planctonic larva to benthic organism is critical and it is during this period than even sub-lethal concentrations of pollutants can greatly interfere with the metabolic activities related to the process of metabolic activities related to the process of metamorphosis.

3- MONITORING WITH BIVALVES

Representatives of the Class Bivalvia are very important for evaluating the level of the pollution of given areas because the group comprises sedentary filter-feeding organisms, which can accumulate xenobiotics

from the environment.

There is however an enormous difference between organisms dwelling on the rocks of the sea bottom at different depths and organisms attached to the rocks of the intertidal zone. The former are strictly dependent on the sediments and the overlying layer of water for their respiratory and alimentary requirements; the latter instead are bound to the surface waters.

The former group lives in a more highly polluted environment than the latter one, due to the fact that many pollutants sink to the sea bottom and are there transformed and accumulated by the various organisms. To give an example, most to the inorganic mercury is biomethylated in the top few millimeters of sediments, where the physical and chemical environment is particularly favorable to the methylation process. The uptake, retention and accumulation of these organic forms by higher living organisms is more likely to occur there.

Most contaminants behave differently once they are within the animal body and therefore a model regarding rate of pollutant uptake-release, of toxicity, of half-life, of concentration factor, and other useful parameters is almost impossible to draw. The "Mussel Watch" program in the United States was set up as an attempt to increase our knowledge of the various factors that significantly influence the turnover of contaminants in the environment (in our case in the sea). This project was designed to calculate the contaminants of the sea-water of the present period and the levels in a 10-20 years time, in order to be able to evaluate the improvement or deterioration of the environment. The exercise was developed by the EPA (United States) and was coordinated by Scientists of the Scripps Institution of Oceanography at La Jolla. During the program many samples of mussels and oysters were collected from 100 localities on the U.S. Coasts. Heavy metals, chlorinated hydrocarbons, petroleum hydrocarbons and radioactive elements were analyzed in the soft parts

of the above mentioned bivalves by different laboratories after careful analytical intercalibration. The results obtained reveal however serious drawbacks to the use of bivalves: one is the variability even between samples collected at close distances; another is the great difference of the concentration factor in the same species taken from waters at similar levels of pollution; another is the seasonal variability even in closely related species. Two examples are sufficient to confirm the existence of various problems with bivalves:

1) copper is metabolized into hemocyanin (Phillips 1976a) and therefore bivalves (and molluscs) are not suitable indicators organisms for this metal;
2) the concentrations of twelve metals in the soft parts of 7 bivalve species living in the same area (Saronikos Gulf at depths between 0 and 12 meters, Papadopolou and Kania 1976) appear quite different from species to species with exceptionally wide ranges (for mercury from 15 to 2,350, or for zinc from 17,000 to 685,000 ppb dry weight).

Taking these difficulties into consideration the "Mussel Watch" promoters, recently suggested developing and building an "artificial or plastic mussels".

In other areas of the world small scale "Mussel Watch" projects have been performed during the last decade and some indications for a general view of the environmental contamination have been obtained.

The data reported by Wolf (1975) analyzing Mytilus edulis from coastal waters of France and England (indicating that high levels of mercury are to be found at the mouth of the Rhine and the Thames and those reported in Bernhard's paper (1981) indicating high levels in Mytilus galloprovincialis collected at the mouth of rivers draining areas rich in cinnabar show that when the sampling is very dense in a given area mussels are quite useful.

On an international basis, following the recommendation of the U.N.

Conference on the Human Environment Program, a Global Environment Monitoring System was set up so that the world might "acquire through monitoring, the data which are needed for the rational management of the environment". Among the UNEP monitoring activities, that of Oceans Monitoring is currently organized through UNEP's Action Plans for Regional Seas; one of the most developed regional monitoring programs is the Coordinated Mediterranean Pollution Monitoring and Research Program (MEDPOL) which, over the last 8 years, has provided a large amount of information. Open ocean and coastal waters have been analyzed, but the monitoring of pollutants, especially in open oceans, has proved both expensive and technically difficult. Much effort was then dedicated to choosing the species to be analyzed taking into account both their suitability for evaluating contaminant levels in various links of the throphic chain and their importance as carriers of contaminants in the human diet. For this reason anchovies, Norvegian lobsters and tuna (or similar high level predator) were chosen, along with mussels (or similar filter-feeder species), and analyzed for the most common highly toxic heavy metals and chlorinated hydrocarbons. The program has attained several goals:

1) unification of methodologies by the different laboratories;
2) attainment of precious information concerning the pollution level of the Mediterranean;
3) confirmation, even with the above-mentioned limitations, of the usefulness of the mussel as "sentinel" for the health of coastal waters.

4- EFFORT FOR THE FUTURE

An ever increasing number of man-produced, often non degradable, substances is produced and soon or later they enter the oceans. Some of them are alien to marine systems, others are part of the terrestrial

and marine systems, but their concentrations increase continuously in the ocean waters as a consequence of man's activities. With the exception of concentrated sources of contamination (hot spots), only few elements or substances are likely to determine highly deleterious consequences "such the tainting of sea-foods, changing the structure of communities of marine organisms, or the loss or restricted use of non-living resources, such as recreational areas (Goldberg 1976)". But even low levels of these substances could be harmful to the environment, inducing very subtle long-term effects. Recent research is mostly oriented toward anticipating substantial modifications of the ecosystem or large tragedies, such as that of the Minamata Bay in Japan. After a period (the last 30 years) of monitoring levels of contaminants in terrestrial and water fauna and of evaluating macroscopic changes in animals populations, a great deal of information is available. However the real impact of one (or more) contaminants on the ecosystem is almost impossible to evaluate. Two examples are sufficient to demonstrate such difficulties; the biological half-life of some metals in mussels kept in an environment contaminated by metals and then moved to clean waters: cadmium 307-1,254 days (Fowler and Benayoun 1976), mercury 337 days (Fowler et al. 1978), selenium 63-81 days (Fowler ans Benayoun 1976), cobalt 57-72 days, zinc 48-76 days, antimony 14-20 days (Waltz 1979), and the discrepancies between the accumulation of chlorinated hydrocarbons in the laboratory and in natural environments.

In natural conditions in fact, many more parameters play a role in the uptake/release process of each contaminant than in a controlled laboratory experiment and the available results (Risebrough et al. 1976) clearly show that the concentration factor by mussels for chlorinated hydrocarbons can vary up to an order of magnitude. Therefore it is impossible to extrapolate from the concentration of a substance in an organism to its amount in the sea-water where the organism has been living. Besides monitoring and evaluating the concentration factor during the last 15

years a great deal of effort has been devoted to various metabolic activities which - indirectly - could give us valuable information concerning the health of the individual, the population, the ecosystem and the entire environment, long before the occurence of irreversible damage.

A recent symposium (1983) held in Woods Hole with the title "Responses of Marine Organisms to Pollutants" proposed to examine our present state of knowledge about "mechanisms and assesment of biochemical, physiological, cellular and histopathological effects of xenobiotics on marine organisms" and to indicate - indirectly - in which direction the future research concerning organisms and environment should go.

Four topics were discussed in great detail:

1) biochemistry of cytochrome p-450 and organic-compound biotrasformation;
2) biochemistry and biological significance of metal-binding proteins;
3) more generalized biochemical and physiological effects including bioassay techniques;
4) effects on immune function and histopathological consequences.

It would take an entire session of this meeting to comment upon the results obtained so far by these new methods for the evaluation of pollution effects; much new information is now available, but many more questions remain to be answered. For heavy metals, studied longer than the recent xenobiotics introduced into the environment by man, Simkiss and Mason's comments at Woods Hole express this new approach to the study of contamination and - in a sense - invite us to shift our courses:"the uptake of certain metals by living marine organisms is governed by first-order kinetics and many of the assumption undertaken during biological monitoring programs are, in fact, valid as a first approximation. Many heavy metals of interest to environmentalists are retained within the tissues by reactive ligands...., some may contribute to a general system of detoxification,..."

whereas others "appear to be integrated into precise metabolic pathways". Within a decade of research in this new direction, indipendantly of the species used for monitoring and/or evaluating the consequences of one or more pollutants to living organisms, the results hopefully will give us some of the answers we badly need:

1) what happens to the various pollutants once they entered the terrestrial estuarine and marine environment?
2) which the relationship between the chemical forms of a given pollutant and their biological effects (animal and man) is?
3) what the sinergistic effects of a chemical (non or slightly toxic when alone, but perhaps highly toxic when combined with others, even not highly polluting, chemicals) are?
4) which the most reliable biochemical method to be used to anticipate the health of an organism (be it a bivalve or another species collected from a well established network of areas around the world) and to prevent serious damages to our environment is?

The answer to these important questions can be only obtained with great scientific and financial efforts; only when these answers are available will it be possible to give more precise indications to legislators of national and international bodies.

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EVALUATION OF THE CARRYING CAPACITY OF MOLLUSCAN SHELLFISH ECOSYSTEMS

M. HERAL *

ABSTRACT Growth of molluscs raised in coastal zones, where the water exchange rate is low, appears to be limited, once a certain biomass level is attained, by the availability of food, making it necessary to determine as accurately as possible the trophic capacity of an ecosystem. This paper analyses the various sources of food for molluscs. It would appear that dissolved organic substances play a major role, providing up to half the energy necessary for their metabolism. Particulate material is filtered by molluscs in proportion to their size, with optimum filtration rates varying with species. The negative effect on meat production of high mineral seston rates is demonstrated, and an analysis provided of the respective role of each component of organic matter. The trophic inflow represented by bacteria and organic detritus is discussed, and phytoplankton rations described. A method integrating current factors is proposed for calculating flows of food, and percentages of phytoplankton retained by molluscs raised in various shellfish-culture ecosystems are presented.

RESUME : La croissance des mollusques cultivés dans les zones littorales, à faible taux de renouvellement d'eau, semble être limitée, au-delà d'une certaine biomasse, par la disponibilité de nourriture ce qui nécessite d'appréhender le mieux possible les capacités trophiques d'un écosystème. Les différentes sources nutritives pour les mollusques sont analysées. Il apparaît ainsi que les substances organiques dissoutes jouent un rôle important pouvant apporter jusqu'à la moitié de l'énergie nécessaire pour leur métabolisme. Le matériel particulaire est filtré par les mollusques, en fonction de sa taille, l'optimum de filtration variant selon les espèces. L'effet négatif sur la production de chair des fortes charges sestoniques minérales est mis en évidence. Le rôle respectif de chaque constituant de la matière organique est analysé. Ainsi les apports trophiques représentés par les bactéries et les détritus organiques sont discutés tandis que les rations phytoplanctoniques sont decrites. En intégrant les courants, une méthode est proposée pour calculer les flux de nourriture, une revue des pourcentages de phytoplancton retenus par les mollusques cultivés dans différents écosystèmes conchylicoles est présentée.

Introduction

As a preliminary, it might be asked why we should study the carrying capacity of waters, i.e. the quantity of food available for molluscs, either in shellfish farms or in some form of intensive culture. From a basin-planning standpoint, it is possible to develop production models for the populations under culture that are derived from models used in halieutics. Such an approach would accordingly not take into consideration the limiting effect of available food quantities, and yet the shellfish industry has developed in estuaries, bays, ponds and relatively closed basins characterized by a high degree of confinement and low water renewal rates. Cloern (1982) demonstrated that, in San Francisco Bay, biomasses of filter-feeding bivalves are large enough to filter a daily volume of water equivalent to the volume of the bay, thus controlling the development of phytoplankton. In the Marennes-Oléron basin, biomasses of oyster and cultivated mussel populations, along with other molluscs, can filter over half the water volume of the basin every day, bearing in mind the standing time for water masses. Table 1 shows that this same volume of water is filtered several times by molluscs.

* IFREMER, B.P. 133, 17390 **La Tremblade**, France

This could explain the relatively low rates ($5\mu g/l^{-1}$ of chlorophyll a) of phytoplankton biomass found in these basins, which are nevertheless very rich in nutrients (Conomos et al., 1979; Héral et al, 1984).

Oyster biomass	Mussel biomass	Biomass other molluscs	Total biomass	Biomass dry weight	Filtration	Daily rate at neap tide	Water volume per tide cycle	Recycling time
70,000 t	3,600 t	5,000 t	80,000 t	2,400 t	$240 \times 10^5 m^3/h$	$576 \times 10^6 m^3/d$	$800 \times 10^6 m^3$	4-9 days

Table 1: Water volume filtered by molluscs in the Marennes-Oléron basin

It is possible that an overall philosophy could be developed to guide planning in these cultivation zones. An empirical approach, i.e. a gradual increase in loads, might show that, past a certain point, production begins to decline, making it necessary to revert to an equilibrium position, although this production-biomass equilibrium can only be determined if the other parameters are constant. The decline in production may, of course, be due to overloading of culture biomass, but also to changes in the cultivation ecosystem involving such things as:

- a rise in bottom levels, causing a slowdown in current and thus of food inflow,
- changes in mineral salt inflows (due to drought, estuary dams, etc.),
- perturbation of phytoplankton growth by pollutants, which also upset mollusc physiology (this is the case, for example, with the organic salt of TBT (Alzieu and Héral, 1985),
- deterioration of shellfish beds through accumulation of organic matter (faeces and pseudofaeces) causing anoxic phases (Kusuki, 1984).

The above elements militate in favour of the overall study of shellfish ecosystems as integrated units. For the purposes of this seminar, we have arbitrarily chosen the following aspect: the food available for molluscs, which is dealt with in this document, i.e. the quantity of food molluscs need to cover their energy, metabolism, growth and reproduction requirements (Deslous-Paoli, 1985), and then the model-building phase, which will enable us to establish relationships between primary and secondary elements (Bacher, 1985).

Many authors have given experimental demonstrations of the role played by various parameters on mollusc nutrition and production. It must nevertheless be admitted (cf. Epifanio et al., 1975, and Dame et al., 1980) that laboratory results are difficult to extrapolate to natural or divergent environments. A study of the carrying capacity of an ecosystem can, however, only take into consideration a certain number of parameters. Initially, therefore, we will attempt to determine relationships observed in the literature in situ between various parameters and filter-feeding mollusc production, in order to propose a list of factors that it appears necessary to study further. We will pay particular attention to the spatio-temporal research procedures which must be developed, in particular for seas characterized by tides.

Relations between biotic and non-biotic water parameters and the production of molluscs observed in situ

A great many authors have demonstrated the influence of temperature. Temperature controls the onset of gametogenesis (Lubet et al., 1981; Héral, 1985) but also its evolution (Mann, 1979). Temperature is also an extremely important parameter which controls all phenomena in mollusc physiology: filtering activity, metabolism and thus respiration and excretion, thus representing a close link with growth in terms of size and weight. This important influence of temperature has made it possible to develop mollusc growth models on the basis of equations by Von Bertalanffy or Gompertz by integrating temperature variations and thus building models of season growth fluctuations: Bachelet (1984) for *Scrobicularia plana*, Bodoy (1982) for *Donax trunculus*, Hamon (1983) for *Mytilus galloprovincialis* (Fig. 1), and Rodhouse et al. (1984) for *Mytilus edulis*.

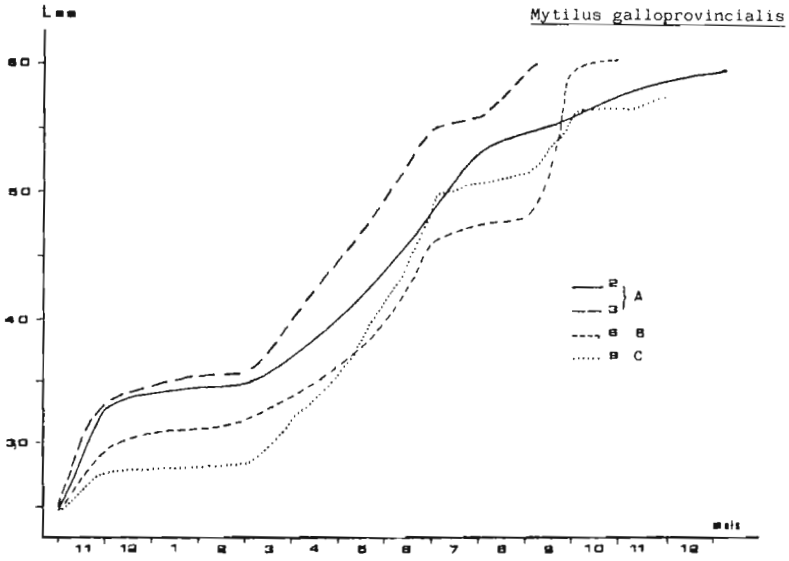

Figure 1: Size-age curves obtained after incorporating temperature and nitrates (Hamon, 1983)

Héral et al. (1984) also demonstrated that, if the egg-laying period is excluded, temperature is the primary explanatory factor for shell growth and the third explanatory factor for meat production. This indicates that other factors play a vital role in meat production. These authors also showed a close link with dissolved carbonated and nitrogenated organic substances as well as with phytoplankton, whether deteriorated (phaeopigments) or in live form (chlorophyll a) in the water or the water-sediment interface (Fig. 2).

Similarly, Lelong and Riva (1976) demonstrated in situ the action of phytoplankton, temperature and salinity on the growth of *Ruditapes decussatus*. A link between benthic biomass and the quantity of chlorophyll was established by Hargrave and Peer (1973), while a logarythmic relationship between ATP content based on current and filter-feeding mollusc production was demonstrated by Wildish et al. (1981). The connection between phytoplankton biomass and weight increase in the oyster *C. gigas* has been confirmed (Deslous-Paoli et al., 1981), as well as a strong correlation between primary production

		WATER														
		T.	Sea	Ses.O	ATP	Chla	Pheo	Prot	Carbh	Fat	C dis	N hum	Bact dis	C hum	A dis	Cl dis	A.A.	N Org
meat	P	0,84	-0,32	-0,41	0,03	-0,25	0,85	-0,18	0,58	0,05	-0,24	-0,25	-0,26	0,98	-0,18	0,21	0,37	0,52
	G	0,28	-0,41	0,06	0,36	0,31	0,58	0,03	0,25	0,05	0,34	0,40	-0,28	0,15	-0,03	0,51	0,72	0,39
shell	P	0,77	-0,36	-0,30	0,19	-0,30	0,31	-0,41	0,20	-0,17	-0,46	-0,42	0,45	0,77	-0,33	-0,04	0,17	0,54
	G	0,87	-0,50	-0,14	0,05	-0,25	0,55	-0,04	0,29	-0,14	-0,28	0,35	-0,09	0,72	-0,72	-0,11	0,57	0,57
Prot.	P	0,89	-0,35	-0,36	0,05	-0,26	0,89	-0,19	0,58	0,02	-0,70	-0,21	-0,23	0,92	-0,15	0,19	0,41	0,55
	G	0,25	-0,37	0,20	0,35	0,32	0,48	-0,02	0,00	-0,05	0,46	0,55	-0,12	-0,13	-0,07	0,33	0,74	0,29
Sugar	P	0,55	-0,24	-0,45	0,05	-0,20	0,54	-0,21	0,52	0,09	-0,25	-0,36	-0,74	0,98	-0,19	0,23	0,18	0,36
	G	0,19	0,02	-0,34	0,19	-0,02	0,24	0,08	0,59	0,29	-0,28	-0,46	-0,19	0,83	-0,18	0,36	-0,23	0,14
Carbh	P	0,54	-0,43	-0,45	-0,07	-0,27	0,58	-0,08	0,61	-0,05	-0,24	-0,15	-0,38	0,89	-0,05	0,23	0,45	0,56
	G	0,20	-0,42	-0,12	-0,08	-0,08	0,43	0,04	0,18	-0,17	0,16	0,48	-0,31	-0,03	0,09	0,10	0,78	0,28
Fats	P	0,59	-0,32	-0,48	0,01	-0,27	0,60	-0,20	0,55	0,03	-0,26	-0,25	-0,24	0,97	-0,17	0,19	0,37	0,46
	G	0,50	-0,51	-0,14	0,27	0,15	0,83	-0,13	0,39	-0,01	0,15	0,08	-0,26	0,54	-0,08	0,53	0,67	0,54

		Water-sediment interface									
		Chla	Pheo	C dis	A hum	Cl dis	Prot hum	Bact dis	Prot dis	Carboh hum	Fa
meat	P	0,43	0,08	0,30	0,17	0,04	-0,03	-0,28	-0,18	0,57	-0,01
	G	0,71	0,45	0,39	0,80	-0,05	-0,29	-0,70	0,44	0,80	-0,44
shell	P	0,34	0,02	0,14	0,01	0,19	0,55	0,15	-0,03	0,47	-0,04
	G	0,75	0,68	0,02	0,16	-0,23	0,21	0,01	0,44	0,35	0,14
Prot.	P	0,53	0,19	0,26	0,22	0,06	0,00	-0,27	-0,11	0,58	-0,01
	G	0,75	0,64	0,74	0,75	-0,13	-0,22	-0,49	0,50	0,37	-0,37
Sugar	P	0,23	-0,10	0,32	0,10	0,03	-0,07	-0,24	-0,29	0,52	-0,05
	G	-0,21	-0,09	0,37	0,00	0,10	-0,09	-0,32	-0,21	0,58	-0,08
Carbh	P	0,55	0,22	0,27	0,27	0,07	-0,10	-0,45	-0,05	0,61	-0,11
	G	0,73	0,70	0,02	0,47	-0,13	-0,28	-0,49	0,32	0,77	-0,31
Fats	P	0,37	0,03	0,27	0,14	0,02	-0,08	-0,37	-0,22	0,54	-0,12
	G	0,75	0,37	0,48	0,74	0,10	-0,17	-0,67	0,22	0,74	-0,37

Figure 2:

Correlation coefficients between water, water-sediment interface and oyster production. P = one-year oyster; G = two-year oyster. 0.6 = significant coefficient on the threshold of 95% r > 0.60

multiple correlations:

shell sm. oysters = 0.18 x water time - 11.45 r = 0.77
shell lg. oysters = 0.14 x chl a in silt - 3.31 (2nd factor T) r = 0.75
meat sm. oysters = 0.014 x dis.C + 0.017 pheo. water - 2.98 (3rd factor T) r = 0.98
meat lg. oysters = 9.64 x hum.silt C + 4.94 amino acids - 19.71 (3rd factor chl a) r = 0.97

and the energy content of *Ruditapes decussatus* (Bodoy and Plante-Cuny, 1983). Kautsky (1982) showed good correlations in *Mytilus edulis* between shell growth and temperature and between shell growth and chlorophyll content, if the gametogenesis period is excluded. Shaffee and Lucas (1982) showed that production yields are negative if chlorophyll and temperature levels are at a minimum.

The harmful effect of excessive seston loads on flesh production was shown by Vahl (1980). This was demonstrated in *Chlamys islandica* by Wildish et al. (1981), for various lamellibranchs by Deslous-Paoli et al. (1981) and by Héral et al. (1983) in adult *Crassostrea gigas*. The importance of bacteria (Prieur, 1981), often associated with particles, was mentioned by Martin (1976) in *Ruditapes decussatus*, by Amouroux (1982) in *Venus verucosa* and by Mengus (1978).

Dissolved organic substances

Although experimental work by Péquignat (1973) demonstrated the nutritional role of amino acids and sugars, the energy contribution they represent has to date not been taken into account in determining mollusc energy balances.

The branchial epiderm of lamellibranchs is the site of high absorption of dissolved organic molecules such as amino acids, sugars and fatty acids. Numerous experimental studies have described these mechanisms, for instance recent articles by Jorgensen (1982-1983, Wright and Stephen (1982), Gomme (1982) and Neil et al. (1983). This absorption mainly takes place in the gills, but also through the stomach and the middle intestine (Stewart and Bomford, 1976; Bomford and Gingles, 1974). The kinetics of this absorption is described using the Michaelis-Menten equation, the constants of which depend on amino acid concentrations present in the ecosystem. Thus *Mytilus edulis* can absorb half of the amino acids in water flowing through the branchial cavity at concentrations of 1 µmole l^{-1} (Jorgensen, 1983). Jorgensen also shows that absorption of amino acids from natural sea water may be sufficient to provide over twice the energy necessary for branchial filtration. Similarly, Wright (1982) estimated that absorption of amino acids contributes 6 to 60%, depending on concentrations available in the water, of the oxydation requirements of metabolism exhausted by respiration. This mechanism makes it possible to satisfy the requirements of 11 amino acids necessary to *Mytilus caoifornianus*, principally L-methionine and L-lyzine-NCl (Harrison, 1976), along with taurine, which represents 70% of the pool of free intra-cellular amino acids in the gills (Zurburg and de Zwaan, 1981). Conversely, Nell et al. (1983) showed that, although active absorption is observed for glucose, the absorption resembles a sort of passive diffusion that makes no major contribution to the carbohydrate requirements of oysters.

Similarly, a certain number of dissolved organic substances may be absorbed through the same metabolic channel and no longer play a role in energy supply, but rather the role of a growth substance like choline chloride or vitamins (Nell et al. 1983). Collier et al. (1953) also showed the very beneficial effect of carbohydrates present in the marine environment on pumping rates and the intervalval activity of oysters. These observations led to the development of the early artificial diets based on sugars, fats and vitamins (Castell and Trider, 1974; Trider and Castell, 1980; Nell and Wisely, 1983).

In coastal waters, dissolved amino acid levels vary between 0.2 and 2 µmole per litre (North, 1975). Jorgensen (1982) found variations in Isefjord

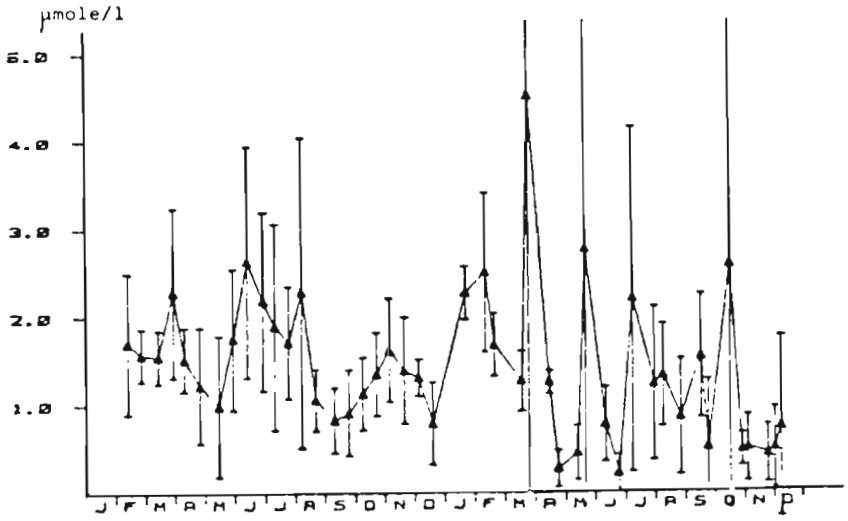

Figure 3: Variations in dissolved amino acid content of waters of the Marennes-Oléron basin (after Héral et al., unpublished)

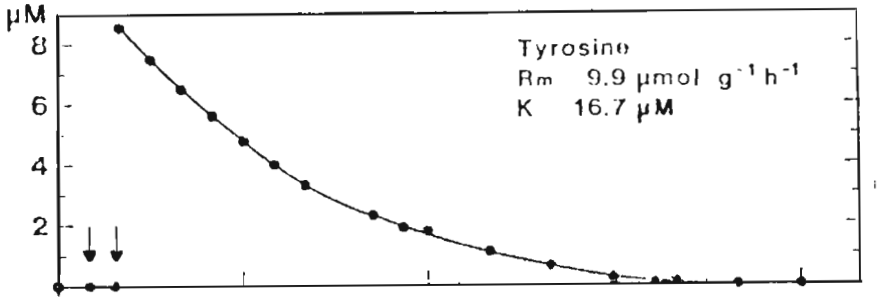

Figure 4: Uptake kinetics of amino acids in *Mytilus edulis* adapted to 50% artificial sea water at 14°C (after Jorgensen, 1983)

Amino acid	N	R_m µmol g^{-1} h^{-1}	K_u µM	R_m/K_u l g^{-1} h^{-1}	Uptake from 1 µM µmol g^{-1} h^{-1}
Glycine	9	9.6±1.1	4.2±0.3	2.0±0.3	1.8±0.2
	4*	18.2±2.0	3.9±0.3	4.7±0.7	3.8±0.5
Glutamic acid	2*	9.6 (8.7, 10.5)	3.2 (3.1, 3.2)	3.1 (2.8, 3.3)	2.3 (2.1, 2.5)
Taurine	3	9.7 (7.4 - 12.5)	5.1 (3.3 - 8.3)	2.1 (1.5 - 2.5)	1.6 (1.3 - 1.9)
Glutamine	4	20.3±3.0	10.4±2.1	2.0±0.2	1.8±0.2
Tyrosine	2	9.9 (9.9, 9.9)	23 (17, 29)	0.5 (0.3, 0.6)	0.5 (0.3, 0.6)

between 0.4 and 2.5 µmole l^{-1}. In the Marennes-Oléron basin, Héral et al. (unpublished) found fluctuations between 0.2 and 10 µmole l^{-1}, but these showed no significant seasonal peaks, and daily variation during a given tidal cycle was greater than annual variation. The same was true for dissolved glucose or dissolved organic and inorganic carbon (Feuillet et al., 1979; Feuillet, pers. comm.). These wide variations may be due to the fact that measurements within the ecosystem are a synthesis of absorption and excretion by molluscs but also by phytoplankton and bacteria.

Suspended particulate matter

- Size consumed by filter-feeding molluscs

Recent use of particle meters (Coulter Counter, Luzex) has made it possible to determine the sizes trapped by the branchial filters of molluscs. It would appear that different species select different sizes. Fifty per cent of the particles retained by *Mytilus edulis* measured 1.5 μ (Silvester and Sleigh, 1984), and for *Cardium glaucum* 50% were 1 μ (Jorgensen et al., 1984), while for the anomia *Monia squarna* 50% were 3.5 μ (Jorgensen et al., 1984) and for *Crassostrea gigas* 50% were 3 μ (Kusuki, 1977; Deslous-Paoli and Héral, unpublished).

Optimum filtration for the oyster *C. gigas* takes place at 8-9 microns, while for *C. virginica* it is 5 microns (Palmer and Williams, 1980), and for mussels it is also 5 microns. These selection differences are not constant, however, and appear to depend on the seston load of the system. Deslous-Paoli and Héral (unpublished) show an increase in retention efficiency for waters with low turbidity for *C. gigas*, and Palmer and Williams (1980) demonstrate the same fluctuations for *C. virginica*. All particles larger than this size will then be trapped by the gills. The upper limit of ingestion is difficult to determine, but Paulmier (1972), examining stomach contents, indicates that particles smaller than 50 μ predominate, while those measuring 50 to 100 μ are frequently found, but particles of 100 to 150 μ are very rare.

It thus appears necessary, when studying particulate matter ingestible to molluscs, to take into account this size criterion and make biochemical analyses of the organic matter using differential filtration. This would yield a more accurate picture of the energy value of the fraction of this matter in estuary environments that can be utilized by molluscs. It has been observed in estuaries that the fraction ranging between 1 and 3 μ, of which only a small proportion is retained by the molluscs, may represent 50% of the total number of particles (Fig. 6). Conversely, nannoplankton smaller than 20 μ is directly related to growth of *Mytilus edulis* in the Gulf of Maine (Incze et al., 1980), while for the same species Rosenberg and Loo (1983), working in northwestern Sweden, found the same close link between nannoplankton and mussel weight increase.

- Seston

The mineral portion of seston may be significant in estuary environments during the winter period, when foreshore sediment is put back into suspension by strong tidal currents and storms, along with inflow from estuaries under high water conditions, allowing the silt plug to be expulsed. This high mineral load causes dilution of particulate organic matter and thus diminishes the energy value of suspended material. This causes molluscs to lose weight, since they must draw on their reserves in order to make up for the deficit. Vahl (1980) offers this explanation for variations in growth rates of *Chlamys islandica*. As well, Deslous-Paoli et al. (1981) and Héral et al. (1983) show the negative effect of seston contents higher than 100 mg l^{-1} on meat production in *C. gigas* and explain this negative production by the high rate of biodeposit mainly composed of pseudofaeces, causing larger amounts of energy to be used for sorting particles, mucus secretion and gill cleaning, at a time when phytoplankton biomass is in short supply.

- Bacteria

Counting aerobic heterotrophic bacteria populations, generally called total microflora, makes it possible to quantify bacteria biomasses, although

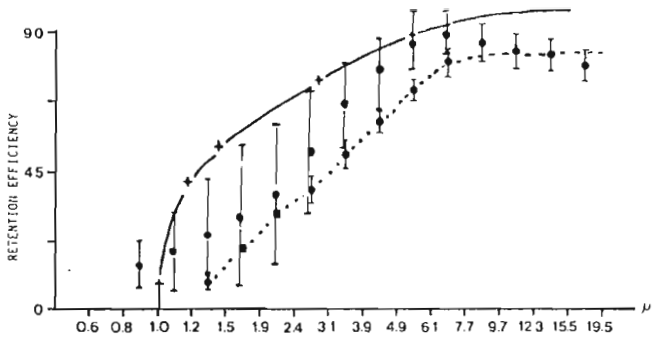

Figure 5: Retention efficiency based on particle size for *Mytilus edulis*+ according to Silvester and Sleigh (1984) and for *Crassostrea gigas* ‡ according to Deslous-Paoli and Héral (unpublished).

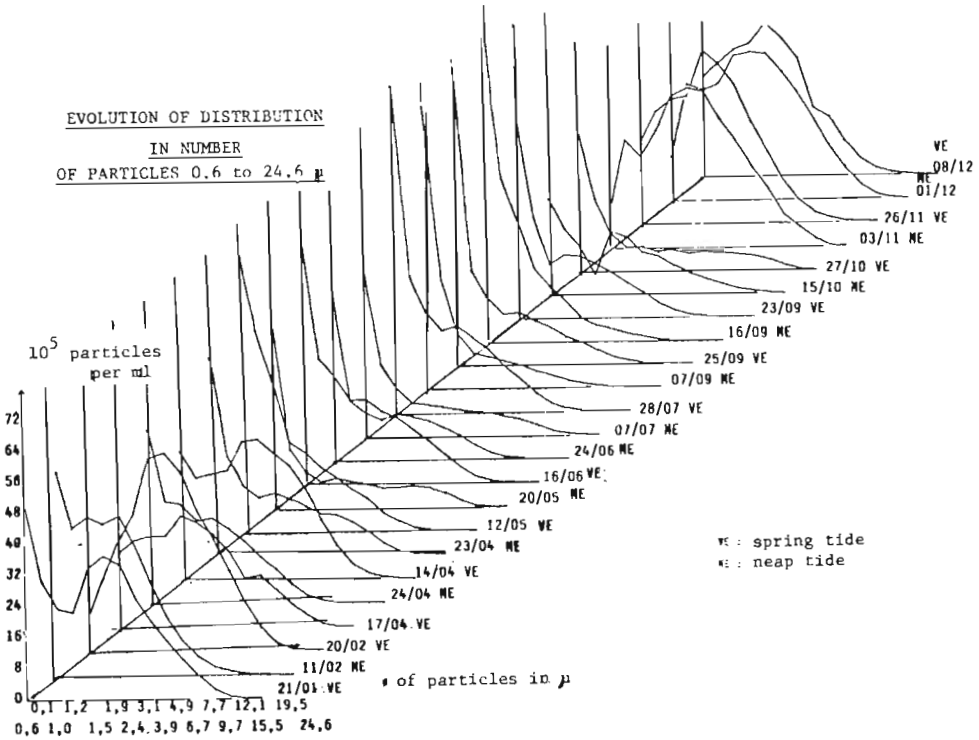

Figure 6: Number of particles according to size in the Marennes-Oléron basin (0.8 to 24.6 μ) (after Héral et al., unpublished)

it is necessary to convert these biomasses into their energy equivalent in order to compare their contribution with that of phytoplankton. Ferguson and Rublee (1976) estimate that, on the average, a bacterium corresponds to 7.8×10^{-5} g of carbon, and this value falls into the range given by Hamilton and Holm Hansen (1967). In the absence of a specific calorimetric coefficient for bacteria, that defined by Salonen et al. (1976) has been applied, i.e. 10.97 cal mg^{-1} of carbon for total aquatic invertebrates. Héral et al. (1983) and Deslous-Paoli and Héral (1984) showed that bacterial biomasses in a shellfish basin represent only a small part of the energy available to filter-feeding molluscs and that there is a high degree of variability between high and low water (Fig.7).

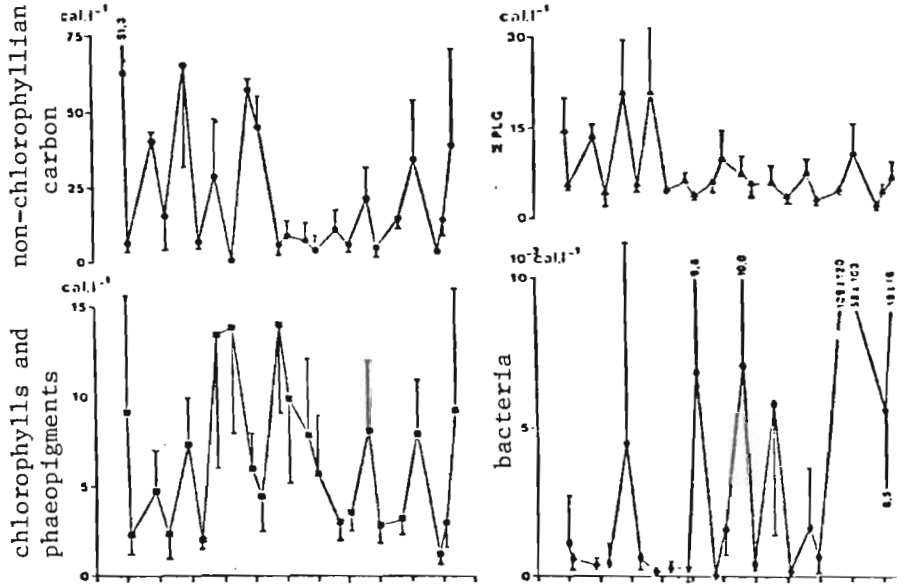

Figure 7: Energy values of bacteria compared to potential food (PLG), phytoplankton biomass (chl*a* + phaeo) and non-chlorophyllian detritus (after Deslous-Paoli and Héral, 1984).

Zobell and Landon (1979), however, presented experimental results showing growth of adult *Mytilus californianus* on bacteria-based diets. Newell (1965) showed that *Macoma balthica* ingests and utilizes bacteria. Similarly Chakroun (1964) demonstrated that mussels concentrate the microflora in their environment. Martin (1978) pointed out that *Venerupis decussata* causes bacterial concentrations in a closed space to decrease by a factor of 7 in five hours, while phytoplankton is simultaneously consumed by a factor of 14. The capacity of bivalves to retain bacteria depends on their state in the natural milieu. Free bacteria are rare, and Sorokin (1981) showed that 30% to 40% of bacterial plankton form colonies of diameters greater than 4 µ and are thus more easily trapped by the branchial filters of filter-feeders, while the remaining bacteria are associated with suspended particles, particularly organic detritus. Lopez (1980), however, demonstrated the active role played by extracts from the crystalline style of *Mytilus edulis* in detaching bacteria from their substratum. Wiebe and Pomeroy (1972) estimate that 2.8×10^6 bacteria per ml would be required to support filter-feeder metabolisms, while Prieur (1981) found that the maintenance ration for a juvenile *Mytilus edulis* should be 1.33×10^6 cells per ml. Such figures may be found in estuaries

(Goulder, 1976; Héral and Prou, 1980), but they are neither constant nor current in natural environments (Prieur, 1981). For adult molluscs, therefore, bacteria appear to be only a complementary ration. The same is true for yeasts, and Epifania (1979), comparing diets with varying proportions of phytoplankton and yeasts, showed that juvenile *Argopecten irradians*, *Mercenaria mercenaria* and *Mytilus edulis* show good growth with a mixture containing 50% yeast. For *Crassostrea virginica*, on the contrary, any increase in the percentage of yeast in diets causes a drop in the growth of meat. Urban and Langdon (1984), working with the same species, confirm that growth in oysters fed with algae-yeast mixtures depends mainly on the quantity of phytoplankton.

Suspended organic matter

Non-living matter may be estimated on the basis of particulate carbon and nitrogen, from which has been subtracted the quantity of carbon and nitrogen of recent phytoplankton origin, as represented by the total amount of chlorophyll *a* and phaeopigments. The remainder thus obtained is multiplied by a caloric coefficient different from that of the plankton, which would overestimate the energy content (Héral et al., 1980). Bernard (1974) proposed 4 cal mg^{-1} of carbon, while Kenchington (1970) found a coefficient of 2.7 cal mg^{-1} of carbon for detritus, Parsons (1963) 5.8 cal mg^{-1} of carbon and Héral et al. (1980) a coefficient of 2.6 cal mg^{-1}. An estimate is thus obtained of the organic carbon of the non-chlorophyllian tripton representing detritus.

Accordingly to Widdows et al. (1979), the sum of the biochemical constituants of organic matter represents an estimate of the potential food for a filter-feeding mollusc. The resulting protides, fats and carbohydrates are multiplied by caloric conversion coefficients described by Brody (1945), which are 5.65 cal.mg^{-1}, 9.45 cal.mg^{-1} and 4.10 cal.mg^{-1} respectively. As for organic carbon content, Telek and Marshall (1974) showed that inorganic carbonates may produce an interference as great as 30% in CHN measuring when samples are rich in highly-carbonated mineral sestons. Héral et al. (1980) reported on the difference between the results of measuring organic carbon by combustion at 900°C and those for organic seston burned at 400°C. The same authors demonstrated that potential food (the sum of protides, fats and carbohydrates) represented only 2.6% of total seston, 16.6% of organic seston and 24.3% of organic matter as determined by CHN. This agrees with the results of several earlier studies (Menzel and Ryther, 1970; Holm-Hansen, 1972; Strickland, 1972; Widdows et al., 1979), which showed that a large proportion of particulate organic matter resists biochemical analysis, while molluscs apparently proportionately use only these reactive forms (Widdows et al., 1979). Notwithstanding the use of coefficients representing two times less energy than those for live plankton, potential food energy represents only an average of 50% of the calories calculated on the basis of organic carbon. The remaining 50% are linked to structural elements that are difficult to account for with biochemical analyses.

Use of detritus by molluscs may take place in two ways (Berry and Schleyer, 1983), either only the microorganisms attached to the detritus are digested and the non-digestible detritus rejected intact in the faeces and replaced in suspension where they may be recolonized by bacteria (Newell, 1965; Darnell, 1964; Odum, 1971), or part of the detritus is digested along with the associated bacteria (Adams and Angelovic, 1960), since the digestive enzymes of molluscs have the ability to utilize them (Bayne et al., 1976).

If we compare the various energy values found by different authors (Table 2), we may observe a certain consistency in the caloric content found in different ecosystems.

False Bay S.A.	Griffith (1980)	6.1 KJ g^{-1} ash-free seston
Linher Estuary G.B.	Widdows et al. (1978)	23.6 KJ g^{-1} protides, lipids, glucides
Ori Reef S.A.	Berry and Schleyer (1983)	19 KJ g^{-1} ash-free seston
Marennes-Oléron	Héral et al. (1980)	0.5 KJ g^{-1} seston 3.6 KJ g^{-1} ash-free seston 21 KJ g^{-1} protides, lipides glucides

Table 2: Energy values of 1 g of seston in selected shellfish ecosystems

- Phytoplankton

Phytoplankton contents follow a seasonal cycle that depends on temperature and on factors that control phytoplankton growth, in particular nitrates and phosphates. Phytoplankton biomasses may be followed by measuring chlorophyll or ATP, as well as by counting the number of phytoplankton cells. The most commonly used data are chlorophyll counts. Biomasses vary from year to year at a given site, depending on inflow from estuaries, and may also vary from bay to bay (Table 3). It may be noted that areas of intenstive mollusc culture show high phaeopigment contents, only 30% of the chlorophyll being active. From a methodological standpoint, this grazing action by molluscs means that phaeopigments must be carefully separated from chlorophylls. It may also be seen that, in areas where mollusc-rearing is the most intensive (Marennes-Oléron, Ria de Arosa), the highest phytoplankton biomasses are found.

It should be borne in mind that, in these coastal environments, the microphytobenthic biomass is from 2 to 25 times greater than the phytoplankton biomass (Zanette, 1980; Robert, 1982), and that any strong tidal currents or severe weather conditions will replace this surface film in suspension, thus making it available to filter-feeding molluscs.

To translate phytoplankton biomass into the energy equivalent, most authors use the factor Organic C = 60 chlorophyll *a* (Strickland, 1960), and then apply the average K-factor of 11.4 cal.mg^{-1} of organic carbon (Platt and Irvin, 1973). The same type of conversion may be applied to phaeopigments, since, although they represent cells that are in the process of breaking down (Héral et al., 1983), they may have the same nutritive value. It is desirable to study these phytoplankton biomasses according to their size and separate nannoplankton, at 3 µ to 20 µ, from phytoplankton at 20-100 µ and 100-250 µ,

which will enable the phytoplankton fraction to be followed in connection with branchial-filter retention efficiency and mollusc growth. Incze et al. (1980) found a direct relationship between nannoplankton smaller than 20 μ and the growth of *Mytilus edulis*, whereas Lassus et al. (comm. pers.), working in the Leucate pond, proved that a chrysophyceae 2 to 3 μ long at 3.2×10^6 cells per litre caused oysters to lose weight and even starve to death.

Location	Chlorophyll *a* $\mu g.l^{-1}$	Phaeopigments $\mu g.l^{-1}$	Σ $\mu g.l^{-1}$	% chlorophyll *a*
Brest Harbour RNO Station 5	m 2.14 max 9.17	m 0.53 max 0.78	2.67	80.1
Gulf of Morbihan Station 4 RNO	m 1.10 max 4.20	m 1.47 max 2.52	2.57	42.8
Marennes-Oléron Station 3 RNO	m 2.35 max 10.08	m 4.25 max 12.2	6.60	35
Arcachon RNO Station 3	m 1.04 max 1.6	m 2.04 max 6.6	3.08	33
Thau RNO Station 3	m 1.19 max 4.00	m 0.77 max 1.63	1.98	60
Ria de Arosa Tenore & Gonzales (1976)	m 7.9 max 40			
Lynher Estuary Widdows et al. (1979)	m 1.4 max 4.0			
Natal, South Africa Schleyer (1981)	m 2.13 max 3.88			
oyster claires Robert (1982)	m 5.12 max 20	m 4 max 0.98	9.12	79

Table 3: Phytoplankton biomass estimated according to chlorophyll a and phaeopigment contents in selected mollusc-rearing areas

A number of experimental studies of mollusc nutrition have been undertaken to get a better idea of the action of phytoplankton and the quantities of phytoplankton molluscs need for growth, reproduction and metabolism. Walne (1970) showed that a great many algae (19) may form the basis for feeding juveniles of *Ostreae*, *Mercenaria* and *Mytilus*. This author later demonstrated (Walne, 1974) that mollusc growth is obtained more rapidly using a mixture of 3 algae rather than one or two algae alone. During a number of experiments being carried out in hatcheries, it became apparent that some algae, when found alone, did not cause any growth. Epifanio (1979), working on 15 diets based on 4 algae, found that size and weight increase were not correlated with total chemical composition nor with amino acid composition, but rather depended on the rate and speed of digestibility of an alga based on its anatomy (theca) as well as concentrations of it in stomach contents (Romberger and Epifanio, 1981). Epifanio et al. (1976) nevertheless also showed that *Thalassomia pseudomona* alone can support growth of

Mercenaria mercenaria, and Flaak and Epifanio (1978) again used this alga, produced in different cultural conditions, with varying sizes and biochemical composition. These authors showed that *Crassostrea virginica* grows more rapidly with a culture medium that is richer in carbohydrates than in proteins. In parallel with these nitrition studies, work was done on an approach to use by molluscs of natural phytoplankton populations, and Héral et al. (1982) showed evidence for consumption of natural populations by *Ruditapes philippinarum*, while Nedhif (1984) described the exhaustion of phytoplankton in basins where this clam was being reared. Zanette and Garnier (1981) gradually eliminated the phytoplankton in claires by increasing the density of cultivated *Crassostrea gigas*, with oyster growth depending on the quantity of phytoplankton consumed.

- Energy balance

If we wish to establish the relation between quantity of food, whether dissolved or particulate, and the energy requirements of mollscs, it must be borne in mind that water masses are in constant movement due to currents flowing over culture areas, and thus bring in a flow of food that will depend on the speed with which the water mass moves. Héral et al. (1983) used the following formula to express this:

$$X = \sum_{i=1}^{n} \frac{Xi \cdot Ci}{n} \cdot T \cdot h$$

where X is the quantity of energy per m^2 and per day of the water column
Xi is the quantity of energy in Kcal or Kjoules per m^3 of a sampling from a tidal cycle
Ci is the instantaneous current at sampling
n is the number of the sample
T is the immersion time of the oyster population
h is the height of water

This formula considers that the mollusc population feeds in a permanent manner during immersion, but many physiological studies have shown that molluscs adapt to discontinuous feeding, either due to immersion or imposed by feeding and digestion cycles (Langton and Gabbott, 1974; Owen, 1974). Langton and McKay (1976) obtained growth in *Crassostrea gigas* by adding food discontinuously, with 6 hours with food and 6 hours without. Higgins (1980) showed that *Crassostrea virginica* seems to be able to detect food levels, and that the quantity of food filtered depends directly upon the time the oysters are exposed to the food. Similarly, Epifanio and Ewart (1977) demonstrated periods of active filtration and periods of quiescence in *Crassostrea virginica*. Copello (1982) observed *Crassostrea gigas* to have a filtration rhythm that was synchronized with the tidal cycle.According to Morton (1970, 1977, 1983) and Langton and Gabbott (1974), tidal rhythm controls the crystalline style of *Ostrea edulis* and *Crassostrea gigas*, causing the crystalline style to dissolve after arrival of food with the rising tide, the substances ingested being digested extra- and intra-cellularly in a cyclical manner depending on the various enzymatic activities related to digestion (Boucaud-Camou et al., 1985). The rhythmic character of digestion thus appears to be a fact, but filtration could remain constant during the period of immersion for intertidal populations. It must, however, be determine what happens during neap tide periods or in tide-less waters, and whether filtration activity is cyclical. If this is the case, the equation above must be modified using a factor based on the duration of feeding.

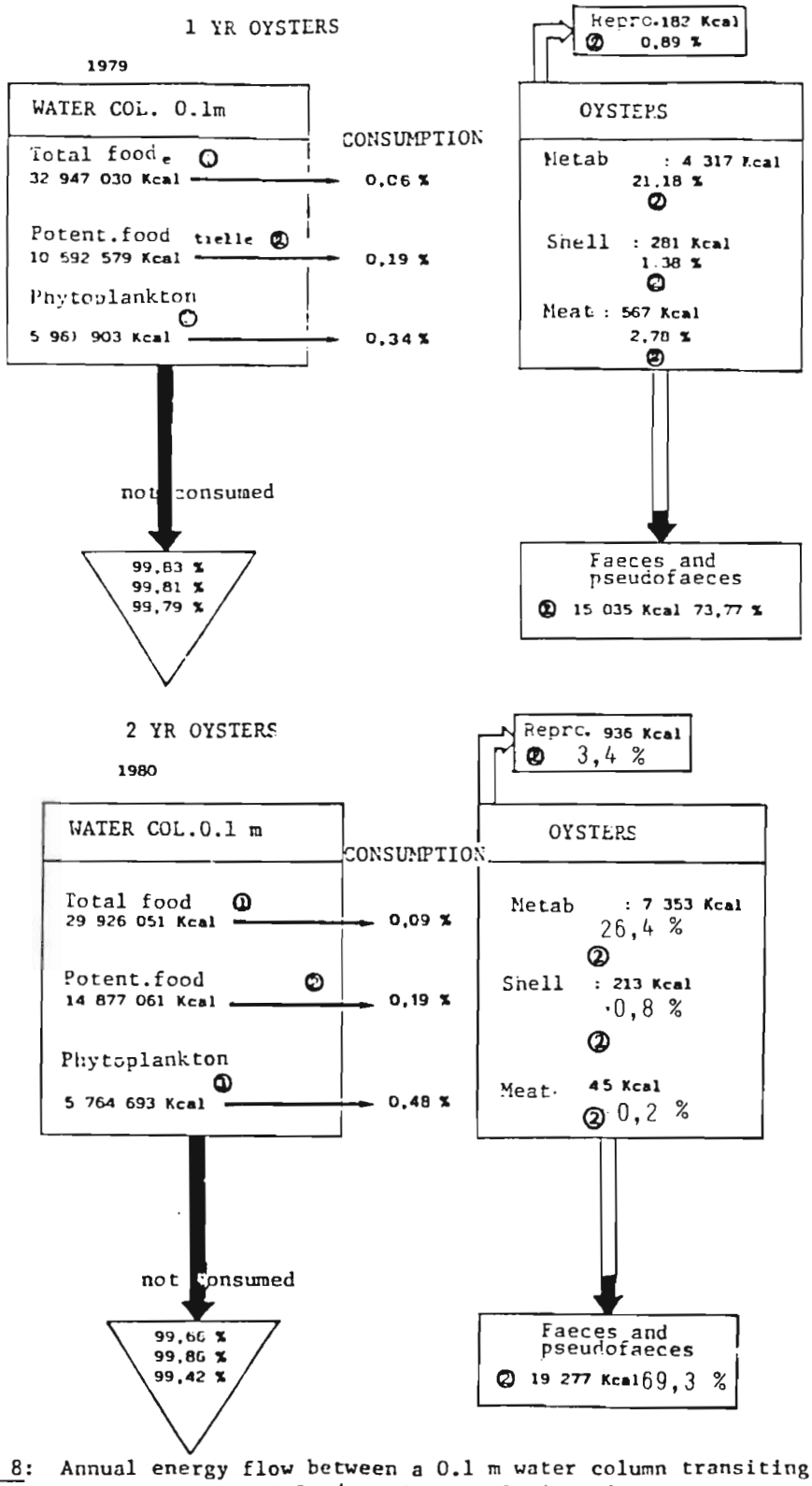

Figure 8: Annual energy flow between a 0.1 m water column transiting at a current of 0.3 m/s and a population of grown oysters at a density of 200 individuals/m^2 (after Héral et al., 1983, and Deslous-Paoli and Héral, 1984).

The relationship between this quantity of available energy and the energy balance of a population of *Crassostrea gigas* was established by Héral et al., 1983, and Deslous-Paoli and Héral, 1984). The energy flow between a water column and the energy balance of 1 m^2 of *Crassostrea gigas* under culture represents only 0.1% to 0.5% of the energy of the water column used by the oysters at an average current of 1 m s^{-1}. If we compare the percentage of phytoplankton use by bivalves at constant current for a constant biomass, it will be seen that, according to various authors, 13% to 90% of the chlorophyll a is filtered by the molluscs, depending mainly on the type of culture (on-ground or suspended).

The production capacity of a sector thus depends on the quantity of food available and mainly on current velocity (instantaneous velocity), but also on the general circulation of water masses in a basin, permitting the water volume used by the molluscs to be changed. This work, which includes a physical model of water mass circulation in a basin combined with a biological model of food consumption, has not yet been published.

authors + site	species biomass in dry weight per m^2	cultures distributed in water section of	% of chlorophyll a retained	current	% retention per m^2 for current of 1 m/s with dry biomass of 1 kg	% retention per m^3 for current of 1 m/s with dry biomass of 1 kg
Héral et al. (1983) Marennes-Oléron (France)	*C. gigas* adult 261 g	0.1 m	2.4%	0.7 m/s	13.1	1.31
Deslous-Paoli and Héral (1984) Marennes-Oléron (France)	*C. gigas* juvenile 65 g	0.1 m	1.5%	0.7 m/s	32.9	3.9
recalculated after Cabanas et al. (1979) Ria de Arosa (Spain)	*M. edulis* 2 yr. 13 250 g	8 m	60%	0.05 m/s	90.6	11.3
Recalculated after Rodhouse et al. (1985) Ireland	*M. edulis* 2 yr 20 000 g	10 m	47%	0.1 m/s	23.5	2.35

Table 4: Percentage of phytoplankton retained by oysters and mussels in selected ecosystems for 1 ms^{-1} current and dry biomass of 1 kg

Apart from the specific model-building problems involved, construction of this model brought with it a number of problems with respect to estimating the carrying capacity of ecosystems.

a) taking into account the food regeneration rate: primary phytoplankton and bacteria production during residual movement of water masses,

b) recycling and reutilization of organic matter from faeces and pseudo-faeces,

c) measurement of biomasses and production over the entire sector under study, which underlies an appropriate sampling strategy, with in particular constant measurements to the limits of the model of the phytoplankton biomass with variations according to day, tides and inflow from estuaries.

Data published to date on the carrying capacity of rearing basins are often more precise as concerns the energy requirements of molluscs, but are still somewhat sketchy with respect to the quantity of food available, with only a few stations normally being studied on a monthly basis. There is considerable trophic variability in these coastal environments, and daily variations in tidal seas is often greater than seasonal variation for a number of papameters. Sampling spread out over a large number of stations makes it possible to assigned to each bay sector a different nutritive value, which is of course well known to operators. Thus any general observations on trophic relations must be obtained through sampling of the characteristics of each bay over a period of time and at various locations.

To conclude this rapid overview of the state of research on determining the trophic value of ecosystems for mollusc production, we may propose the following recommendations:

- improve strategies for sampling nutrients,

- include in energy balance calculations the contribution of nitrogenated and carbonated dissolved organic substances,

- greatly increase the number of current measurements and the number of physical models of residual circulation of water masses,

- examine the recycling of bio-deposited organic matter by molluscs being cultivated,

- seek to develop continuous measurement of phytoplankton biomasses (fluorimeter) and primary production (DCMU)

- develop studies of phytoplankton biomasses according to particle size, with emphasis on nannoplankton,

- increase measurements of in situ consumption rates in ecosystems with weak current regimes.

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ASSESSMENT OF ENERGETIC REQUIREMENTS OF REARED MOLLUSCS AND OF THEIR MAIN COMPETITORS

J.M. DESLOUS-PAOLI *

ABSTRACT : To predict the potential production of a cultivated ecosystem, it is mandatory to know the seasonal changes in energy balance of cultivated organisms. The allocation of energy is controled both by endogenous and exogenous parameters. Two complementary approachs are discussed, the first is ecological and the second is physiological. This synthesis show that in situ studies must be developed especially on biodeposition, and estimation of aerobic and anaerobic metabolism, and, that the estimations of mucus secretion and nitrogen excretion have been often negliged and must be improved. In the near future, if we want to deal with the integrated studies of a shell fish ecosystem and its modelisation, it is mandatory to study alltogether the biochemical, physiological and dynamical parameter not only for individuals but also for population level as well as the quantity and nature of potential food consumed by molluscs.

Key words : Energy balance, filter feeder molluscs, bibliographie synthesis.

RESUME : *Evaluation des besoins énergétiques des mollusques cultivés et de leurs principaux compétiteurs : pour prédire la production potentielle d'un écosystème cultivé, il est nécessaire de connaître les changements saisonniers de la balance énergétique des organismes cultivés. Ces changements sont le résultat de la variabilité de l'environnement, non seulement en ce qui concerne la température, mais aussi et sans doute de façon plus significative de la disponibilité en substances nutritives (Bayne et Newell, 1983). Dans le contexte de l'aquaculture en mer ouverte, les saisons et la courantologie jouent un rôle à la fois sur la qualité et la quantité de nourriture disponible pour les mollusques. Dans cette synthèse nous ne parlerons que de la nourriture particulaire.*

La répartition de l'énergie est contrôlée à la fois par des paramètres endogènes tels que l'âge des individus, les classes de taille et l'état physiologique des organismes, et par des paramètres exogènes telles que la quantité et la qualité de la nourriture, le température, la salinité, l'exondation, etc. Deux approches complémentaires du bilan énergétique sont discutées en fonction des fluctuations des paramètres du milieu. La première, écologique, concerne la répartition des ressources entre les différentes productions (tissu, coquille, gamètes, etc) pour des populations naturelles ou cultivées et leurs variations saisonnières. La deuxième, physiologique, définit, par des études expérimentales, les causes principales de la variabilité des processus physiologiques de production. Cette synthèse montre que, d'une part, les études in situ doivent être développées particulièrement pour les estimations fines de biodéposition, de dépenses métaboliques aérobies et anérobies, que d'autre part, les estimations de sécrétions de mucus et d'excrétions urinaires ont trop souvent été négligées et doivent être affinées.

Ainsi, si nous voulons mener à bien des études intégrées sur les écosystèmes où sont cultivés des mollusques et les modéliser, il est néssaire d'étudier à la fois les paramètres biochimiques, physiologiques et dynamiques non seulement des individus mais aussi des populations cultivées et sauvages mais aussi la qualité et la quantité de la nourriture consommée par ces mollusques.

Mots clés : Bilan énergétique, mollusques filtreurs, synthèse bibliographique

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* IFREMER, B.P. 133, 17390 **La Tremblade**, France

INTRODUCTION

In the context of aquaculture in open sea, the amount and quality of food are variable according to the season and the physical flux in the ecosyst (carrying capacity ecosystems). Thus, to predict the potential production of a cultivated ecosystem, it is mandatory to know the seasonal changes in energy balance of cultivated organisms. These changes result from the environmental variability either in the temperature or, more significantly in the nutrients supply (Bayne and Newell, 1983).

The techniques of physiological energetics allow to understand the adaptation of the energy balance in bivalve molluscs and to calculate the complete energy budget all over the seasonal variations of the field. Such studies are few, they include research on individual organisms or on a whole population. These researchs have been done on *Scrobicularia plana* (Hughes, 1970), *Crassostrea gigas* (Bernard, 1974 ; Kim, 1980 ; Héral et al., 1983 ; Deslous-Paoli and Héral, 1984) *Mercenaria mercenaria* (Hibbert, 1977), *Mytilus edulis* (Bayne and Widdows, 1978 ; Widdows, 1978 ; Rosenberg and Loo, 1983 ; Thompson, 1984a ; Hawkins et al., 1985), *Mytilus chilensis* (Navarro and Winter, 1982), *Perna perna* (Berry and Schleyer, 1983) and a gastropod competitor *Crepidula fornicata* (Deslous-Paoli et al., 1985).

The synthesis on physiological energy has been done by Bayne and Newell (1983) on molluscs (bivalves and gastropods). Here we will try to make a complementary synthesis especially on oysters which are with mussels the main species of cultivated mollusc, with reference of one trophic competitor *(Crepidula fornicata)*.

In this synthesis, we only speak about particulate matter as food. The dissolved substances and their uses by suspension feeding bivalves are not discussed here, because nobody take it into account in the energy budget, although the use of dissolved A.A. and carbohydrates have been proved on *Mytilus edulis* (Pequignat, 1973 ; Jorgensen, 1982, 1983 ; Wright, 1982) and on *Saccostrea commercialis* (Nell et al., 1983).

1. THE COMPONENTS OF THE ENERGY BUDGET

The equation of energy budgets for marine benthic invertebrates was first discussed by Crisp (1971). This equation describes the net energy exchange in the individual organisms under steady state conditions :

$$C = P + R + F + U$$

with $P = Pg + Ps + Pr + Pe$ (Lucas, 1982) and $F = F' + F''$

where C (consumption) is the energy content of food consumed ; P (production) is the energy incorporated in Pg (growth of somatic flesh), Ps (secretory products such as organic parts of the shell, mucus, byssus), Pr (reproductive products) and Pe (eliminated products), R is the energy equivalent of metabolic heat looses, F is the energy content of the not ingested food and not absorbed one that is voided respectively as pseudofeces (F') and feces (F''), U is the energy of excretion products like urine.

In the diagram of figure 1, we show that in bivalvia the ingested energy (I) is the filtrated food (C) which passes through the mouth ($I = C-F'$). The efficiency with which the filtrate ration was ingested is the ingestion efficiency (I/C). The ingested ration is difficult to estimate in marine lamellibranchita, because of the difficulty to separate pseudofeces (F') and feces (F'') especially for species with siphons. Thus in the main study, especially for studies made on the field, the absorption efficiency (Ab/C)

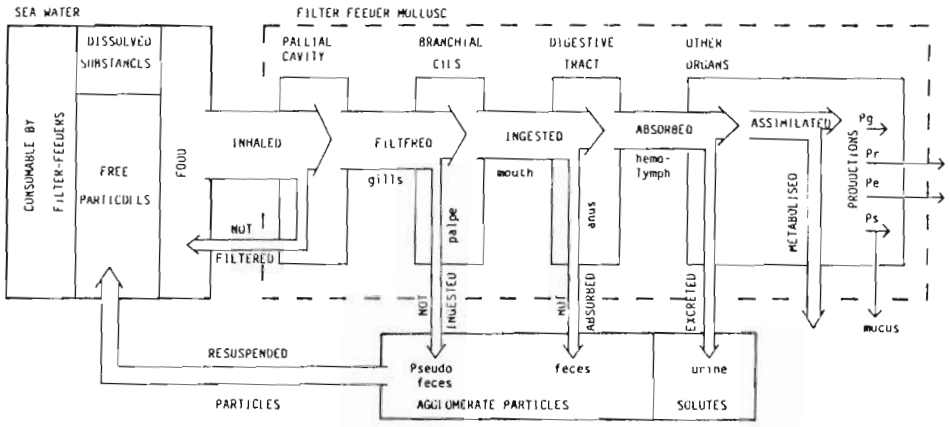

figure 1 : Synthetic diagram fo the energy flow between food and filter feeding molluscs (redraw from Lucas, 1982).

is calculated from the filtrated energy (C) (Widdows, 1978) and not from the ingested one (I) and the absorbed ration is Ab = C - F = I - F''. From the absorbed ration, Bayne and Newell (1983) define two main sources of loss which are the loss of products of protein metabolism (U) and those to the heat increment (R'). Unlike Bayne and Newell (1983) the mucus is not considered as an excretory product (U) but as secretory product like shell and/or byssus (Ps). R' (heat increment) and R'' (metabolic energy losses) are never separated and constitute the total metabolic loss (R = R' + R'') (Bayne and Newell, 1983) which is the oxygen consumption. The assimilated ration (As) can be expressed as As = R + P = C - F - U, where the energy available for production (P) is partitioned between somatic growth (Pg), secretory products (Ps), production of gametes (Pr) and eliminated products (Pe) (Lucas, 1982). This last term (Pe) is not taken into account for individual energy balance, except when flat fish eat the siphon of *Scrobicularia plana* for exemple (Hodgson, 1982).

Some confusion arises between absorption and assimilation in a number of papers. This is due to the fact that the excretion product (U) was often neglected. The definition of efficiencies has been reviewed for its ecological interest (Lucas, 1982) and physiological interest (Lucas and Shafee, 1983).

$$\text{Assimilation efficiency} = \frac{As}{C} = \frac{P + R}{C} = \frac{C - F - U}{C} = \frac{P + R}{P + R + F + U}$$

$$\text{Gross production efficiency} = \frac{P}{C} = \frac{Pg + Pr + Ps + Pe}{C} = \frac{P}{P + R + F + U}$$

$$\text{Net production efficiency} = \frac{P}{As} = \frac{Pg + Pr + Ps + Pe}{As} = \frac{P}{P + R}$$

$$\text{Gross growth efficiency} = \frac{Pg}{C} = \frac{Pg}{P + R + F + U} = \frac{Pg}{Pg + Pr + Ps + Pe + R + F + U}$$

$$\text{Net flesh growth efficiency} \quad \frac{Pg}{As - Pg} \qquad \frac{Pg}{Pr + Ps + Pe + R}$$

2. POPULATIONS ENERGETICS

A review of the population energy budget has been done by Bayne and

Table 1 : Basis components of the population energy budgets of marine suspension and deposit feeders in percent of consumed energy. Mean values calculated ignoring the values for *Tellina tenuis* and taking values for only years 2 and 10 for *Patinopecten* and *Chlamys* respectively.
(from Bayne and Newell, 1983)

Organism	Feces (F)	Absorbed ration A = (C − F)	Gross production efficiency P_g	+ P_r	= P/C	Respiration (R)	Net respiratory cost (R/A)×100	Urine (U)	Net production efficiency (P_g+P_r)/A ×100	Reference
Mercenaria mercenaria	58.7	41.3	5.6	4.7	10.3	18.7	45.3	12.3	35.5	Hibbert (1977)
Ostrea edulis	30.7	69.3	6.4	5.5	11.9	29.0	28.4	—	17.2	Rodhouse (1979)
Scrobicularia plana	39.3	60.7	6.6	6.2	12.8	47.9	21.0	—	21.0	Hughes (1970)
Macoma balthica	40.0	60.0	—	—	18.0	42.0	70.0	—	30.0	Warwick et al. (1979)
Patinopecten yessoensis (yr 1)	21.1	79.9	39.7	1.6	41.3	39.2	49.1	—	24.9	Fuji and Hashizume (1974)
P. yessoensis (yr 2)	34.6	65.4	21.8	4.9	26.9	43.6	66.7	—	40.8	Fuji and Hashizume (1974)
P. yessoensis (yr 3)	32.5	67.5	19.6	8.2	27.8	47.9	70.9	—	41.2	Fuji and Hashizume (1974)
Tellina tenuis	90.0	10.0	1.0	0.8	1.8	6.7	67.0	—	18.0	Trevallion (1971)
Aulacomya ater	41.5	58.4	—	—	9.2	49.2	84.2	—	15.7	Griffiths and King (1979a, 1979b)
Hydrobia ventrosa	37.0	63.0	—	—	21.0	20.7	32.8	—	33.3	Kofoed (1975b)
Chlamys islandica (yr 5)	66.6	33.4	11.0	1.7	12.7	20.7	62.0	—	37.9	Vahl (1981b)
C. islandica (yr 10)	74.2	25.8	2.6	2.7	5.4	20.4	79.2	—	20.8	Vahl (1981b)
C. islandica (yr 15)	74.8	25.2	1.4	3.3	4.8	20.4	80.9	—	4.8	Vahl (1981b)
Mytilus edulis	54.0	45.9	8.9	4.8	13.7	25.8	56.1	6.4	29.8	Bayne (unpublished)
Mean ± SD	45.6 ± 14.0	54.4 ± 14.0	8.7 ± 6.8	4.8 ± 1.2	14.4 ± 6.6	33.0 ± 12.6	53.7 ± 23.0	—	27.1 ± 8.8	
Carnivores										
Navanax inermis	35.4	64.6	17.9	13.6	31.5	28.1	43.4	7.0	48.7	Paine (1965)
Polinices duplicatus	12.8	87.2	31.9	9.0	40.9	46.2	53.0	—	46.9	Huebner and Edwards (1981)
Archidoris sp.	48.0	52.0	37.0	—	37.0	—	—	—	71.1	Carefoot (1967b)
Mean ± SD	32.0 ± 17.8	67.9 ± 17.8	28.9 ± 9.9	—	36.5 ± 4.7	37.1 ± 12.8	48.2 ± 6.8	—	55.6 ± 13.5	

Table 2 : Annual energy budget of filter feeders molluscs calculated for field population in percent of consumed energy

Organism	Pe	Pg	Ps	Pr	R	F'	F''	U	As/C	P/As	Auteurs
Mytilus edulis		33.4			46.5	20		-	80	42	Rosenberg and Loo, 1983
Perna perna		19.3		3.4	19.1	58		-	42	55	Berry and Schleyer, 1983
Crassostrea gigas		4.5		18.2	18.2	54.5		4.5	41	56	Bernard, 1974
Crassostrea gigas	2.1	15.3	0.4	2.7	35	17.2	27.3	-	56	37	Kim, 1980
Crassostrea gigas 1	-	2.8	1.4	0.9	21.1	73.8		-	26	19	Deslous-Paoli and Héral, 1984
Crassostrea gigas 2	-	0.2	0.8	3.5	23	72		-	28	16	Héral et al., 1983
Crepidula fornicata		4.6		1.6	0.8	48	45	-	55	13	Deslous-Paoli et al., 1985

1 1 year old oysters 2 2 old years yosters

Newell (1983) where all the components are expressed in percent of consumption (C) (table 1). We added some new results in the table 2 which exclusively concerns field studies.

In that case, the production is not only influenced by growth of individuals but also by the immigration of new ones. Losses are due to mortality emigration and the reproductive effort of the whole population (Verhagen, 1982). The input of energy from immigration happened in Pg and Ps whereas the output of energy from mortality and emigration act on Pe, and the reproductive effort on Pr.

For exemple, Rodhouse et al. (1984) compared the resource allocation in two population of *Mytilus edulis*, one is cultivated, the other is wild, when the total cumulative production is approximately equal. They define considerable differences in resource allocation (fig. 2) which are mainly due to the structure composition of the two population (fig. 3). In the cultivated population, all the mussels are young (less than eighteen month old) with very low reproductive effort (Pr) and high somatic production (Pg). In the wild population the highest proportion of old mussels with very high reproductive effort (Pr) and low somatic growth (Pg) invers the resource allocation in the production. Therefore the study of énergy budget of a population must be done in the same time that structure and dynamic study of the population.

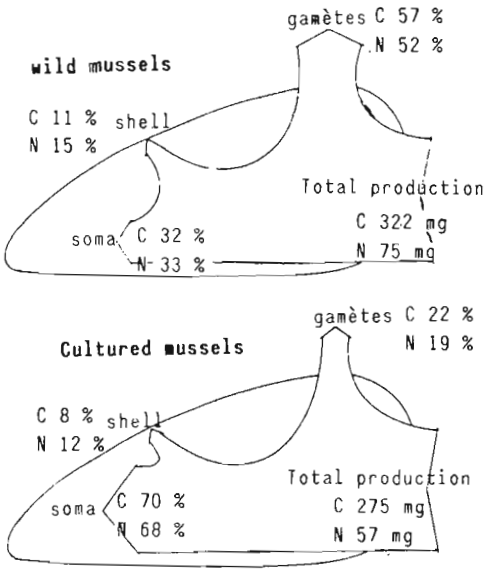

Figure 2 : *Mytilus edulis* : Allocation of carbon and nitrogen in wild and cultured mussels (from Rodhouse et al., 1984).

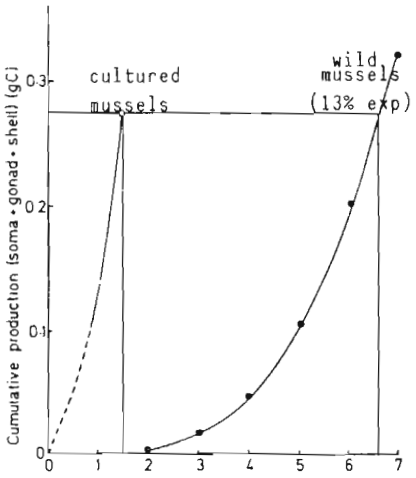

Figure 3 : *Mytilus edulis* : cumulative production of wild and cultured mussels (from Rodhouse et al., 1984).

Steady state condition are rarely encountered for population because of the continuously increasing or decreasing of biomass depending to the season, it is preferable to calculate monthly energy budgets rather than annual ones (Lucas and Shafee, 1983). Nevertheless some of the components of the equation are difficult to determine on the field (C, U, R). They necessit experimental determination. But the application of laboratory-based studies to the field situation presents many problems (Bayne and Newell, 1983). these problems are related in laboratory to consumption and absorption under differents trophics level and differents trophics quality, to respiration and excretion with starved or not starved organisms and to the physiology of the organisms test in laboratory.

3. PARAMETERS ACTING ON PHYSIOLOGICAL ENERGY

3.1. Field study

Some endogenous parameters act on the physiological energy, the age or the size class and the seasonal physiological state of an organism.

Rodhouse (1978) finds an age dependant annual repartition of energy in *Ostrea edulis* (fig. 4) as, Vahl (1981) for *Chlamys islandica* and Deslous-Paoli et al. (1985) for *Crepidula fornicata* according to the position along the chain. As the individual ages, a greater proportion of P is due to the gametes production (Bayne and Newell, 1983) and the somatic tissues (Pg) and shell product (Ps) declines to zero. When the animal has reached its maturity (Salzwedel, 1980) the net production efficiency may become relatively constant but the energy input in Pr increases (fig. 5) and in the older organisms, the allocation of all available surplus energy on the production of gametes (fig. 6)

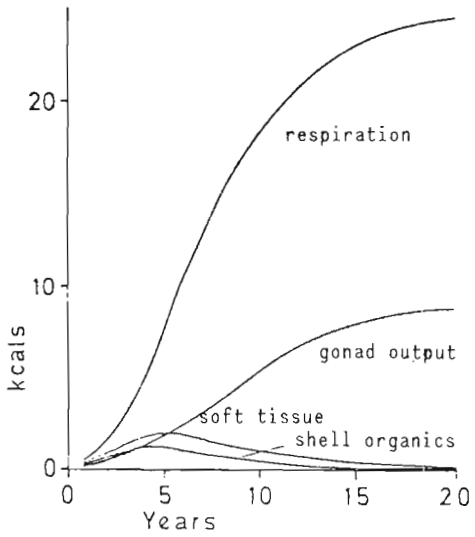

Figure 4 : Age-dependent annual production of soft tissue, shell organics, gonad output and respiration in an oyster *Ostrea edulis* (from Rodhouse, 1978).

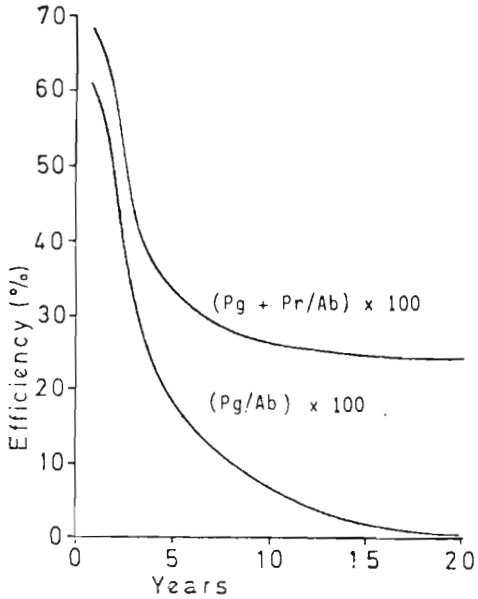

Figure 5 : Net growth efficiency (Pg + Pr/Ab) and net growth efficiency of somatic tissue (Pg/Ab) in oysters *Ostrea edulis* (from Rodhouse, 1978).

ultimately sets the limits on size (Bayne and Newell, 1983). The relationship between the net growth efficiency and size of organism (fig. 7) is identical to the one concerning the age. When a population is studied, the population structure must be taken into account to allocate energy to Pg and Pr (fig. 8) It is mainly due to a different mortality rate between younger and older individuals and the middle ones.

The physiologicaly dependend partition of energy is mainly due to period of gametogenesis (fig. 9). For some molluscs, such a *Mytilus edulis*, somatic and gonadal growth occurred at different time. This is not the case for *Crassostrea gigas* which must perform at the same time, in spring and summer somatic growth and gametogenesis (fig. 10 - 11) (Kim, 1980 ; Héral et al., 1983 ; Deslous-Paoli and Héral, 1984). Shafee and Lucas (1982) give a detailled analysis of the reproductive effort of *Chlamys varia* as well as Vahl (1981) for *Chlamys islandica*. Depending on the season, the energy used

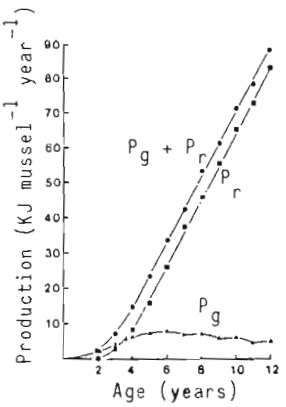

Figure 6 : *Mytilus edulis*. Somatic production (P_{gi} ▲), gamete production (P_{ri} ■) and total production ($P_g + P_{ri}$ ●) in individuals from Bellevue (from Thompson, 1984b).

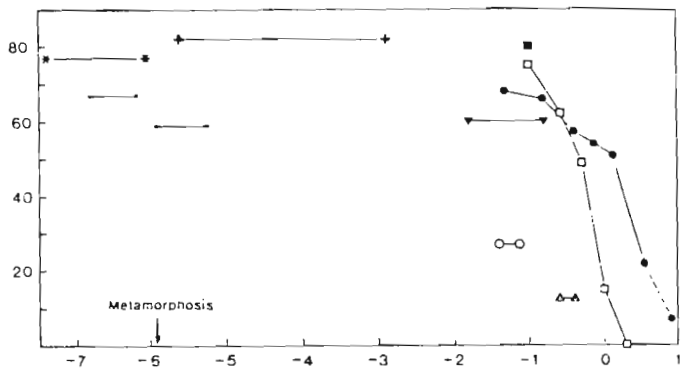

Figure 7 : From Jorgensen, 1976.

Relationship between body weight and net growth efficiency in *Mytilus edulis*.

- * Veligers. Isefjord, Denmark, June (Jorgensen, 1952).
- · Veligers and young post-metamorphic stages, growth in the laboratory (Bayne, 1965). Oxy consumption from Zeuthen (1947).
- + Øresund, Denmark, summer, recalculated from Thorson (1946, p. 460). Oxygen consumpti from Zeuthen (1947).
- ● La Jolla, Calif., USA, August-November (Coe, 1945). Oxygen consumption from Thompson Bayne (1974), highest level.
- ▼ Oslo fjord, Norway, August-September (Bøhle, 1970). Oxygen consumption from Thompson Bayne (1974), highest level.
- □ Norfolk, England. Maximum values obtained in laboratory (Thompson & Bayne, 1974).
- ■ Mass., USA, feeding ^{14}C-labelled *Dunaliella tertiolecta* (Gilfillan, 1975).
- ▲ Mass., USA, aquaculture experiments (Tenore et al., 1973).
- o Weser Estuary, FRG, maximum values in laboratory (Winter, 1974).

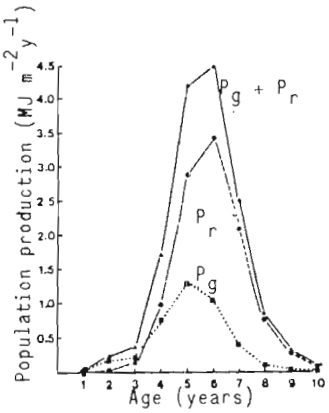

Figure 8 : *Mytilus edulis*. Production by the population at Bellevue. ■ somatic production $(P_g)i$ ● gametes production $(P_r)i$ ▲ total production $(P_g + P_r)$ (from Thompson, 1984b).

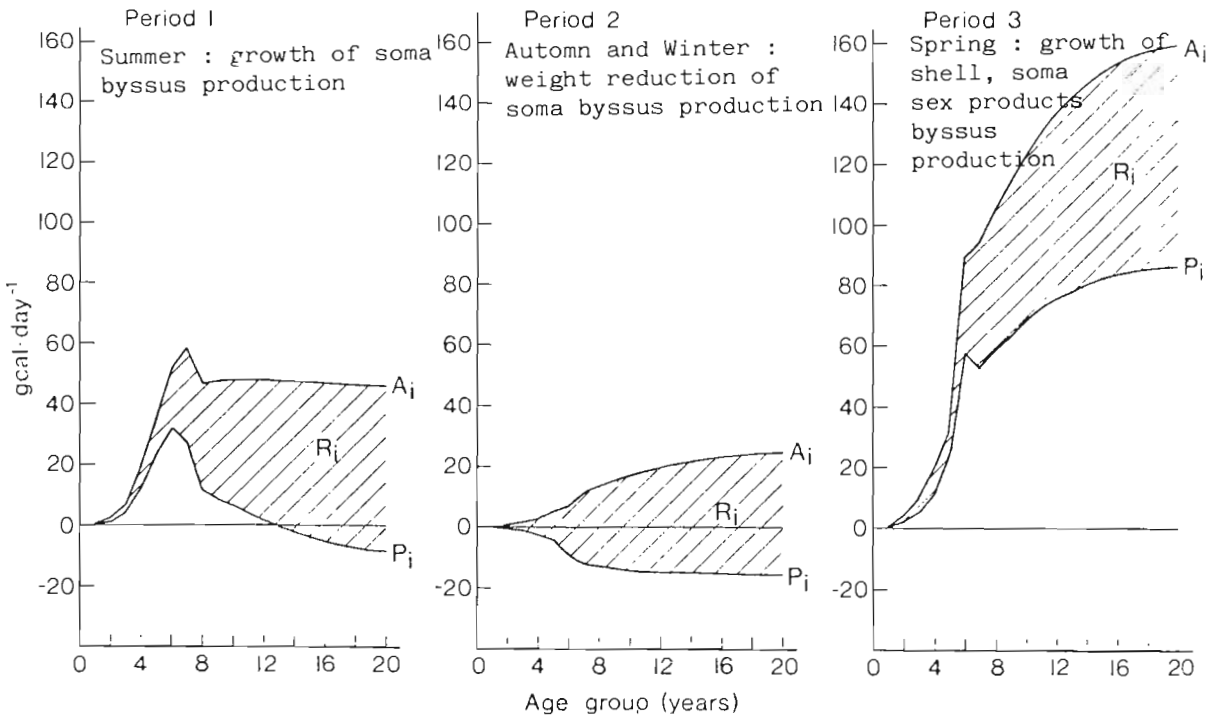

Figure 9 : Age-specific energy budget of *C. islandica* in summer, autumn and winter, and in spring (from Vahl, 1981).

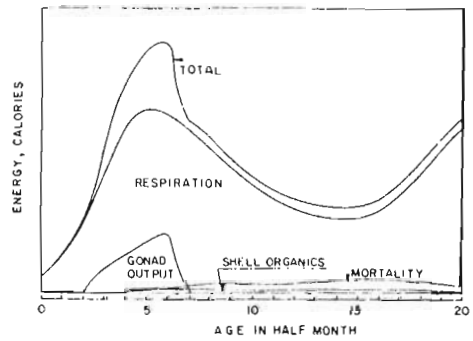

Figure 10 :Age specific distribution of energy loss by oysters population. (from Kim, 1980).

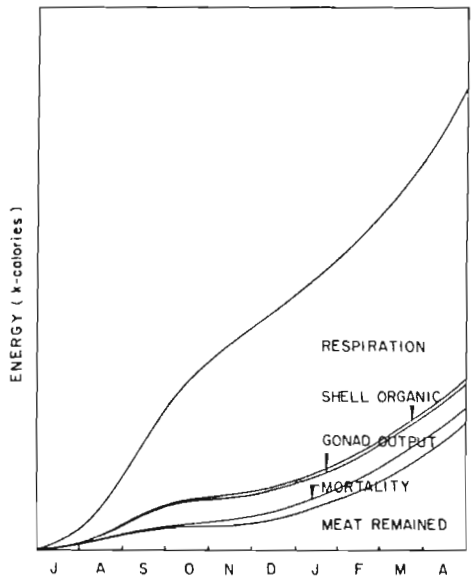

Figure 11 : Cumulative energy used by the population of the oyster *C. gigas* in the culture bed (from Kim, 1980).

to produce gamete is taken either from endogenous food reserves (september) of from exogenous food (june) because at that time somatic and gonadal growth occurred together.

In each species the endogenous parameters (gametogenesis and growth) and the exogenous parameters (temperature, food) are closely related, set in seasonal context, and condition both the reproductive effort and the timing of reproductive events (Sastry, 1979 ; Newell et al., 1982) *Mytilus edulis* populations cultivated in different places, where the environmental stress are more or less reduced, have differently developped there reproductive efforts (fig. 12)

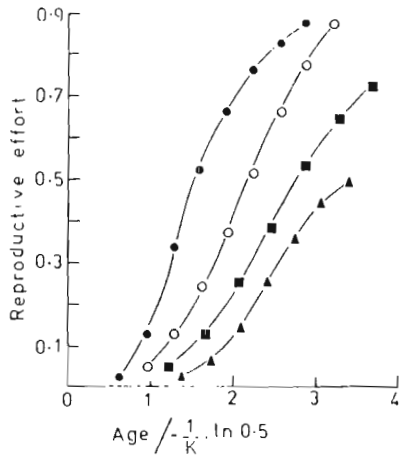

Figure 12 : Reproductive effort calculated as Pr/P of *Mytilus edulis* from four populations, related to age standardized for growth rate. ● Bellevue, Newfounland. (from R.J. Thompson, unpublised date). ○ Lynher ; ■ Mothecombe ; ▲ Cattewater. (All southwestern England ; from Bayne and Widdows, 1978 and Bayne et al., 1983). (from Bayne and Newell, 1983).

The impact of environmental changes (Zandee et al., 1980) depends on the age or size of individuals as Thompson (1984a) see on *Mytilus edulis* (fig. 13) about scope for growth. The younger *Crassostrea gigas* does not exhibit a negative growth during winter (Deslous-Paoli and Héral, 1984) whereas the two years old *Crassostrea gigas* shows negative growth during the same season (Héral et al., 1983) (table 3), smaller individuals were more able to compensate the metabolic energy losses, than the larger one. This is linked with the energy expended for food intake by filtration (Bayne and Newell, 1983). The older mollusc can not obtain their maintenance ratio from natural food must use their endogenous reserves.

Storage of carbohydrates, lipids and proteins usually occurs during spring when food is abondant, and for some species, such carbohydrates reserves are immediatly used for gametogenesis (Gabbot, 1976). For others species, these reserves will be used in winter to ful-feel the metabolic requirements when the food scare. As suggested by Sundet and Vahl (1981) for *Chlamys islandica*, the younger individuals of *Crassostrea gigas* invest in rapid growth, during a more longer period than older one, with the risk to not possess large reserves for winter food storage. In contrast, mature *Crassostrea gigas* stop their growth one month before spawning (August), first because all the available energy production is utilized for gametogenesis as Barber and Blake (1981) said for

Table 3 : Daily energy balance of oysters cultivated at density of 200 per square meter. Oysters settle in july 1978. (Redraw from Heral et al., 1983 ; Deslous-Paoli and Heral, 1984). Values in Kcal.

Date	Pg	Pr	Ps	R	F	P	A	C
12.02.79	0,07	-	0,04	0,572	0,10	0,11	0,68	0,78
28.03.79	0,13	-	0,03	0,742	1,10	0,16	0,90	2,00
25.04.79	0,52	-	0,09	2,845	1,69	0,61	3,46	5,15
28.05.79	1,51	-	0,31	7,065	1,18	1,82	8,89	10,07
26.06.79	5,53	-	0,99	15,108	2,09	6,52	21,63	23,72
24.07.79	8,97	-	2,96	25,106	34,79	11,93	37,04	71,83
21.08.79	2,73	6,49	0,72	17,441	116,07	9,94	27,39	143,46
24.09.79	2,81	-	0,98	18,521	93,54	3,79	22,31	115,85
22.10.79	-0,69	-	2,18	14,249	22,76	1,49	15,74	38,50
20.11.79	-0,99	-	-0,20	13,909	6,37	-1,19	12,72	19,09
18.12.79	-0,34	-	1,02	15,443	36,66	0,68	16,12	52,78
21.01.80	-0,79	-	0,02	11,40	108,9	-0,77	10,63	119,53
20.02.80	-0,43	-	0,02	10,26	15,5	-0,42	9,84	25,34
17.03.80	-4,50	-	0,70	13,09	450,9	-3,80	9,29	460,19
1.04.80	3,28	-	1,56	21,45	29,4	4,84	26,29	55,69
1.05.80	2,71	-	0,56	22,60	24,1	3,27	25,87	52,97
2.06.80	6,92	-	0,26	27,62	13,1	7,18	34,8	47,90
15.07.80	2,71	21,78	2,93	38,64	83,0	27,42	66,06	149,06
25.08.80	2,77	16,75	0,49	26,61	77,6	20,01	45,62	124,22
22.09.80	-1,86	-	1,02	24,82	64,7	-0,84	23,98	88,68
27.10.80	-12,08	-	-0,27	18,52	72,4	-12,35	6,17	78,57
24.11.80	-0,57	-	1,70	15,65	53,5	1,13	16,78	70,28
23.01.81	-0,73	-	-0,22	14,43	10,5	-0,95	13,85	24,35

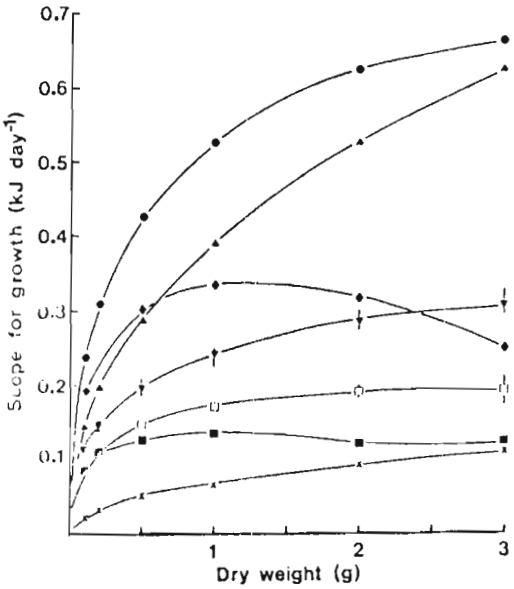

Figure 13 : *Mytilus edulis*. Scope for growth as a function of dry weight (●) 16th October 1980, (▲) 24th June 1980, (♦) 28th july 1980 (▼) 19th December 1979, 12th March 1980, 10th september 1980 (mean + range), (□) 7th November 1979, 22nd January 1981 (mean + range), (■) 29 th April 1980, (x) 11th December 1980. (From Thompson, 1984a).

Argopecten irradians, and secondly to store reserves after spawning to winter.

The use of available food on the field seems to be related with the quantity and the quality of the particulate food, Widdows and al.(1979a) give a schematic diagram summarising the effect of particle concentration on feeding and digestive system (fig. 14). The pseudofeces production occurs when a threshold concentration of seston is reached in water (Foster-Smith, 1975). In the field, it is difficult to separate pseudofeces production (F'') and feces production (F') and the two are usually considered together as biodeposition. Sornin et al. (1983) describe a relationship between seston concentration and the amount of biodeposition product by *Crassostrea gigas* (fig. 15). Up to 97 % by weight of processed material may be rejected from the mantle cavity (Hylleberg and Gallucci, 1975). An annual mean of 75 % of the energy filtered, as protein, lipid and carbohydrate, is rejected as biodeposition by *Crassotrea gigas* (Héral et al., 1983 ; Deslous-Paoli and Héral, 1984) whereas only 45 % is rejected by *Crepidula fornicata* (Deslous-Paoli et al., 1985). For *Crepidula fornicata*, the seasonal biodeposition represent from 26 per cent of the filtered energy in june, to 68 % in december. For *Crassostrea gigas* in Marennes-Oléron the energy loss by feces and pseudofeces can represent up to 98 % of the consumed energy in winter with hight seston concentration and only 9 % during spring. In this study, the values of consumption are underestimate because urine and mucus was neglected. It reveals the importance of the seasonal availability and quality of food on the absorption efficiency of molluscs, but also of the grazing system (radula or not) between species.

If it is possible to estimate directly on the field the production P and the total biodeposition (F) and their fluctuations due to the environmental variations, laboratory experiments are necessary to quantify the losses dues to heat metabolism (R) and excretion (U) and the actual input of food through the filtration (C) and ingestion (I) rate of individuals.

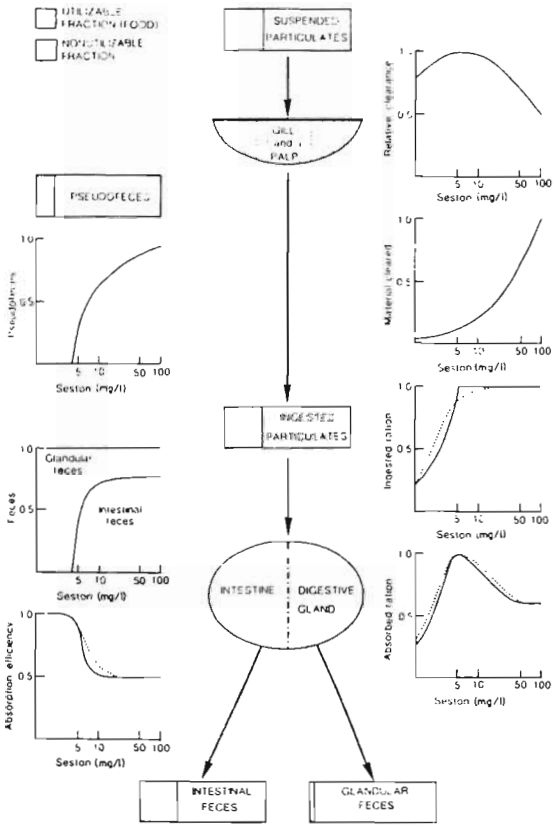

figure 14 : *Mytilus edulis*. Schematic diagram summarising effect of particle concentration on feeding and digestive system (from Widdows et al., 1979a).

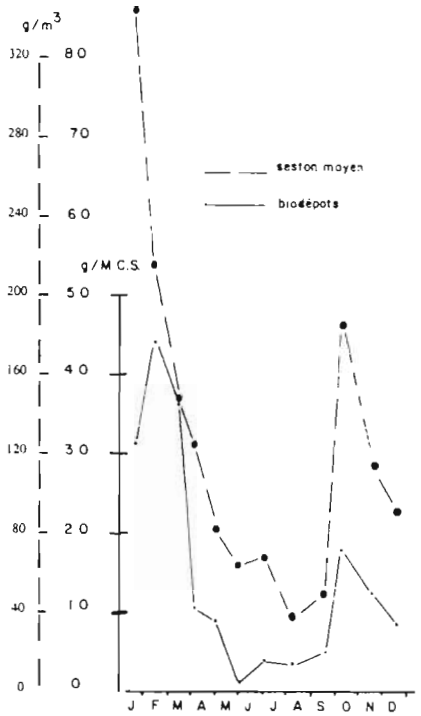

Figure 15 : Seasonal evolution of biodeposit product by *Crassostrea gigas* (g/g dry flesh weight) and of average seston (g/m^3) (from Sornin et al., 1983).

3.1. Laboratory experiments

3.2.1. Energy intake

There is no doubt that filtration and retention rate are related to the dry body weight (See Bayne and Newell, 1983 for a synthesis), to the flow rate (Møhlenberg and Rüsgard, 1979), to the particulate concentration in sea water (Epifanio and Edward, 1977 ; Wisely and Reid, 1978 ; Winter, 1978 ; Widdows et al., 1979a ; Palmer and Williams, 1980 ; Lee and Chew, 1981 ; Fiala Medioni and Copello, 1985) (fig. 14) and to the size or volume of celes and particles used as food in laboratory study (Kusuki, 1977 ; Wisely and Reid, 1978 ; Jorgensen et al., 1984) (fig. 16).

In contrary, diurnal and tidal rhythms of filtration are not really defined and depend on species. Some authors have found them (Salanky, 1966 ; Morton, 1971 ; Palmer, 1980a) and some others not (Winter, 1978 ; Higgins, 1980). In the same way it is still difficult to control the size or quality of particle selection ability. At high seston concentration, particle selection occurs when the threshold of pseudofeces production is over (Kirboe and Mohlenberg, 1981) and will be performed by the labial palps (Bernard, 1974 ; Thiesen, 1977).

Therefore a relative enrichment of energy in the ingested food is observed in front of energy of filtrate particulate matter (Haven and Morales-Alamo, 1966 ; Kiorboe et al., 1981 ; Newell and Jordan, 1983). At low seston concentration, the retention efficiency increases (Palmer and Williams, 1980 ; Fiala Medioni and Copello, 1985) (table 4) for the finer particles, either with an hypersecretory of mucus on the gills (Palmer and Williams, 1980) or with a variation of the diameter of the gill ostia by changes of the blood pressure in the gill filaments (Elsey, 1935) or by muscula action (Dral, 1968).

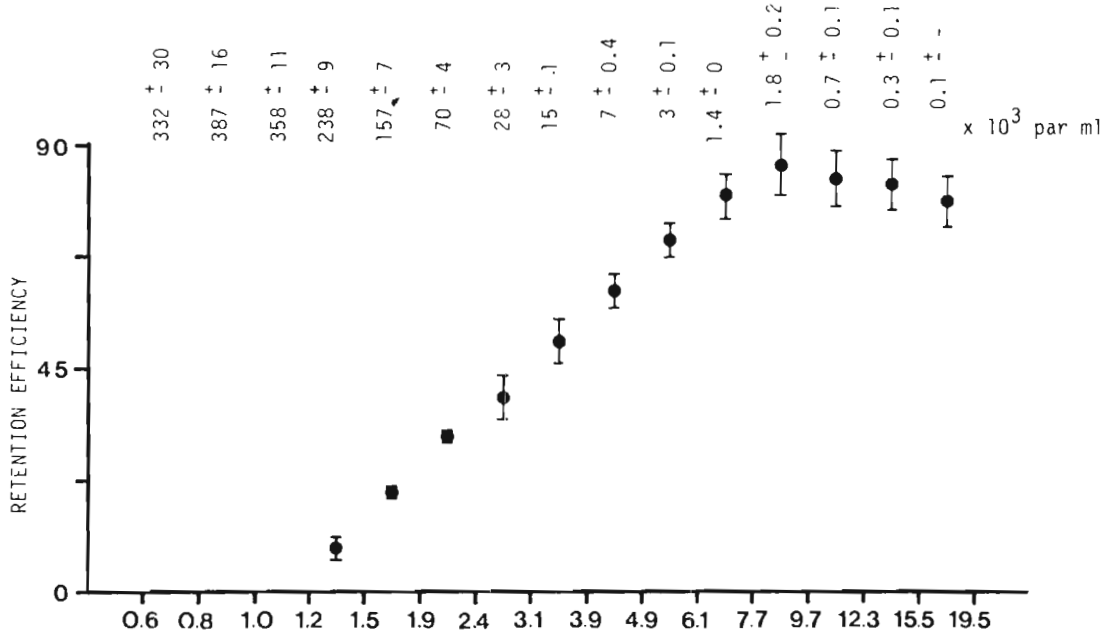

Figure 16 : Efficiency of particule retention by *Crassostrea gigas* with natural food in may, values are means ± standard deviation. Values on the top are means of particle concentration in seston (x 10^3 par ml) (Deslous-Paoli and Héral unpublish data).

The table 4 shows an increased variance when the retention efficiency increases for smaller particles in *Crassostrea gigas* (Deslous-Paoli and Héral, unpublised data) *Cerastoderma edule* (Vahl, 1973) and *Crassostrea virginica* (Palmer and Williams, 1980 ; Palmer, 1980a), even though this efficiency is nearly constant with *Argopecten irradians*. This mechanisms may serve to maintain an optimum of ingested material (Davenport and Woolmington, 1982) and a continuous digestion (Palmer, 1980b). Figure 17 gives schematic aspects of the relationship between filtration, ingestion and assimilation rate (Navarro and Winter, 1982 ; Wilson, 1983) for *Mytilus chrilensis* where B is the food density at which an optimum amount of food is ingested.

Assimilation efficiency is usually not dependent of body size and the main factor affecting it is undoubtedly the quantity and nature of ingested food (Griffiths and King, 1979a ; Gerdes, 1983a). For *Crassostrea gigas* the assimilation rate remains constant over a wide range of food concentration when the filtration rate decreases (Gerdes, 1983a) as well as *Crassostrea virginica* (Langefors and Maurer, 1975) *Mytilus chilensis* (Navarro and Winter, 1982) *Modiolus modiolus* and *Artica islandica* (Winter, 1969) (fig. 17). But if the filtration rate remains constant, the assimilation efficiency is still dependent on algal concentration, as for *Mytilus edulis* (Widdows, 1978) and *Aulocomya ater* (Griffiths and King, 1979a) (fig. 18).

Table 4 : Efficiency of particle retention of *Crassostrea gigas* under hight natural seston (20/2/84 ; 19/3/84 ; 14/5/84) and low natural seston (27/2/84 ; 27/3/84 ; 22/5/84) in relation with temperature.( ) : standard deviation. (Deslous-Paoli and Heral, unpublish data).

Date	20/2/84		27/2/84		19/3/84		27/3/84		14/5/84		22/5/84	
	rétention %	nb particules $x10^3$ - ml^{-1}	rétention %	nb particules $x10^3$ - ml^{-1}	rétention %	nb particules $x10^3$ - ml^{-1}	rétention %	nb particules $x10^3$ - ml^{-1}	rétention %	nb particules $x10^3$ - ml^{-1}	rétention %	nb particules $x10^3$ - ml^{-1}
0.6-0.8	0	-	0	556 (20)	0	291 (13)	7.4 (1.8)	829 (31)	0	332 (30)	0	745 (23)
0.8-1.0	0	-	1.2 (6.7)	207 (18)	0	360 (8)	6.7 (2.5)	322 (41)	0	387 (16)	14.4 (7.5)	343 (23)
1.0-1.2	0	60 (3)	7.4 (1.7)	91 (8)	0.9 (1.4)	350 (5)	6.5 (8.9)	70 (11)	0	358 (11)	18.3 (12.5)	123 (24)
1.2-1.5	0	74.5 (2.6)	6.4 (8.9)	53 (4)	6.3 (4)	221 (7)	8.3 (10.3)	22 (3)	8.6 (2.2)	238 (9)	24.2 (18)	45 (17)
1.5-1.9	1 (2)	80 (1)	14 (5.9)	28 (3.3)	13.6 (9.6)	159 (7)	15.3 (12.1)	12 (1.5)	20.3 (1.5)	157 (5)	29.2 (24)	19 (2)
1.9-2.4	16 (3)	56 (1.6)	22.5 (9.4)	10 (2.4)	19.5 (14)	73 (5)	26.4 (12.5)	6 (0.7)	31.2 (1.5)	70 (4)	37 (23)	11 (1)
2.4-3.1	29 (3)	32 (1.6)	32.4 (10)	4.2 (0.8)	26.9 (5.2)	36 (1.4)	41.6 (12)	3 (0.3)	39.1 (5.0)	28 (2.5)	49.6 (19)	6 (0.7)
3.1-3.9	39 (3)	14 (1)	42.9 (9.5)	2.4 (0.3)	39.2 (5.5)	17 (1)	41.3 (7.3)	3 (0.3)	50.1 (4.4)	15 (1.2)	55.5 (14)	3 (0.3)
3.9-4.9	50 (1)	5.5 (0.4)	53.1 (10)	1.2 (0.1)	51.7 (6.7)	7 (0.5)	48.7 (8.4)	1.1 (0.2)	60.1 (3.8)	7 (0.4)	76.1 (12)	1.6 (0.1)
4.9-6.1	65 (2)	2 (0.2)	62.1 (11.8)	0.6 (0.1)	62.3 (5.3)	2.7 (0.2)	58.5 (15.6)	0.3 (0.1)	70.4 (3.7)	3 (0.1)	84.9 (9.1)	1.1 (0.1)
6.1-7.7	76 (4)	0.8 (0)	64.6 (11.9)	0.3 (0)	71.8 (5.2)	1 (0.1)	64.8 (12.5)	0.2 (0)	79.9 (4.8)	1.4 (0.1)	89.5 (7.7)	0.8 (0.1)
7.7-9.7	78 (8)	0.2 (0)	64.1 (9.3)	0.2 (0)	78.9 (7.1)	0.6 (0)	72.2 (9.4)	0.2 (0)	85.7 (6.2)	1.8 (0.2)	82.4 (9.0)	0.2 (0)
9.7-12.3	-	-	-	-	74.4 (10.5)	0.2 (0)	66.3 (17.3)	0.1 (0)	83.2 (5.8)	0.7 (0.1)	-	-
12.3-15.5	-	-	-	-	67.6 (11.6)	0.1 (0)	51.2 (31.8)	0.02 (0)	81.6 (5.1)	0.3 (0.1)	-	-
15.5-19.5	-	-	-	-	69.1 (6.4)	0.1 (0)	-	-	78.9 (5.2)	0.1 (0)	-	-
seston mgl^{-1}	-	10	-	4	-	7.56	-	2.93	-	8.16	-	2.07
température °C	8°C		5°C		11°C		10.5°C		14°C		17°C	

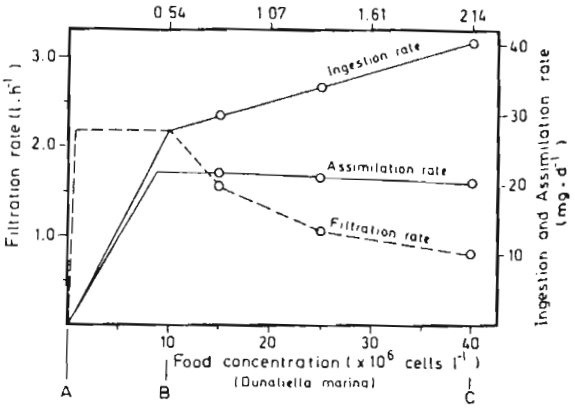

figure 17 : *Mytilus edulis*. Concept of the interrelationships existing between filtration rate, assimilation rate, and food concentration (from Navarro and Winter, 1982)

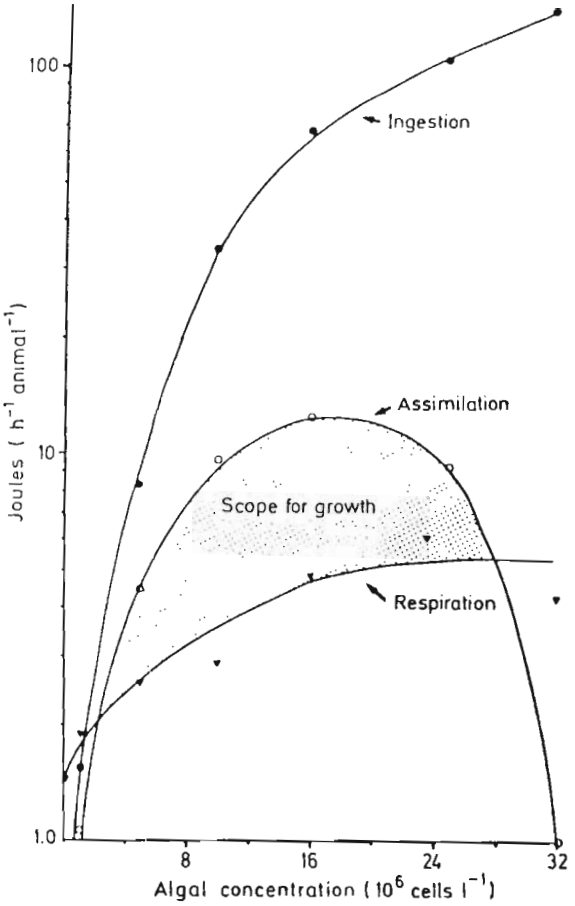

Figure 18 : *Aulacomya ater*. Ingestion ration, assimilation ration, oxygen consumption and scope for growth in 50 mm mussels, expressed as functions of food concentrations (from Griffiths and King, 1979a)

But some differences appear between assimilation efficiency measured for *Perna perna* on the field (42 %) and in laboratory (61 %) (Berry and Schleyer, 1983). Nevertheless, Hawkins et al. (1985) find that the absence of resuspended bottom material, which has been found to stimulate rates of both absorption and growth (Winter, 1976, 1978 ; Kiorboe et al., 1981) does not affect the bioenergetic steady-state evident among mussels. These findings conform with those of Riisgard and Randlov (1981) who reported that a "restricted" diet of *Phaeodactylum tricornutum* enables *M. edulis* from Denmark to grow at rates comparable with those found in nature. But for *Crassostrea virginica*, Urban and Laigton (1984) suggest than kaolinite may improved oyster growth by increasing digestion efficiency.

3.2.2. Metabolic costs

Energetic costs of metabolism can be calculated from the consumed oxygen (Gnaiger and Forstner, 1983), from the released carbon dioxide, or from the produced heat. The energetic equivalent of oxygen consumption varies according to the substrate being used by the animal. Estimates of energy flow based on oxygen consumption generally assume a mean oxycaloric equivalent of 20.08 J/ml O_2. For a review on the oxygen consumption in oysters see Shumway (1982). Metabolic energy expenditure is affected by a large range of endogenous

factors (body size, gametogenic stage, activity) as well as by environmental factors (temperature, salinity, oxygen availability, exposure to air, food availability) (Bayne, 1976 ; Widdows, 1978 ; Newell and Branch, 1980 ; Bayne and Newell, 1983).

For *Crassostrea gigas*, the metabolic rate is related to body size by on allometric equation (Lee and Chew, 1981 ; Gerdes, 1983b) (fig. 19) as well as for the others suspension and deposit feeders (Jorgensen, 1976 ; Newell et al., 1977 ; Rodhouse, 1978 ; Navarro and Winter, 1982 ; Hamburger et al., 1983). The average relationship defined from suspension and deposit feeders, is $Y = 0,5\ X^{0.73}$ (Bayne and Newell, 1983) where y is the oxygen consumption and X the body size. But, in order to compare the metabolic rate of organisms, the consumption of O_2 is related to the unit of body weight. It shows that energy flow through small individuals or species may be much greater than might otherwise be supposed on the basis fo their biomass alone.

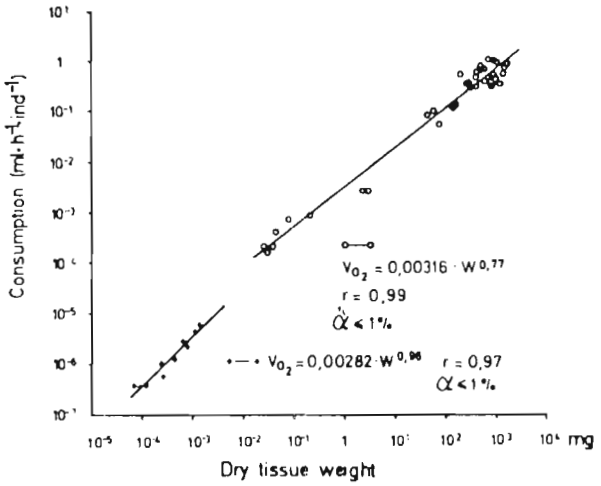

Figure 19 : *C. gigas* : relationship of oxygen consumption and body size (dry tissue weight) in oysters and oyster larvae (from Gerdes, 1983b).

An increase in oxygen uptake associated with reproduction has been found in *Mytilus edulis* (de Vooys, 1976) as well as in *Chlamys islandica* (Vahl, 1978). Hawkin et al. (1985) have correlated the fluctuations in oxygen consumption with the reproductive cycle and use of stored reserves for *Mytilus edulis*. Mori (1968) has studied the relationship between tissues and oxygen consumption during sexual maturation and spawning for *Crassostrea gigas* and has suggested that carbohydrates are more efficient as an energy source than fats in gill, digestive diverticula and pallial margin.

Experiments on rate of oxygen consumption are difficults to compare because some ones concern active or routine rates with fed organisms and some others performed on starved organism and concern basal or standard metabolic rates. The standard rates of oxygen consumption represent approximately half of the active rate (Dame, 1972 ; Bayne et al., 1976 ; Shumway and Koehn, 1982). For a given species, the rate of oxygen consumption also varies according to the temperatures within its thermal tolerance. Studies on the effect of temperature on oxygen consumption of oysters (Dame, 1972 ; Newell et al., 1977 ; Kim, 1980) show either a limited capability or no possibility for adaptation or acclimation, as for *Mytilus edulis* (Griffiths, 1980). Identical results

were found for temperature salinity combinations (Shumway and Koehn, 1982). Energy losses from metabolism are compensated by changes in the feeding rates (Hughes, 1980 ; Fiala Medioni and Copello, 1985). For *Crepidula fornicata*, Newell and Branch (1980) have suggested that an adjustment of feeding rate and metabolic energy expenditure can occur in response to environmental temperature change.

For oysters and mussels, some relationship between oxygen consumption and feeding activity have been found by Collier (1959) ; Thompson and Bayne (1974) Bayne et al. (1976) ; Griffiths and King (1979a) Navarro and Winter (1982). Bayne (1985) summarises the differents levels of the metabolics costs in figure 20. The energetic costs of feeding activity are associated with filtration activity, movments and energetic requirement of ingestion and absorption (Jorgensen, 1976) and Jorgensen (1982) shows that for *Mytilus edulis*, the energy of dissolved aminos acids absorbed by the gills which are pratically only epidermal structures, correspond to 1.5 times the metabolic requirement of beating cilia. Such a cost has been defined for *Mytilus chilensis* as a fonction of body weight (Navarro and Winter, 1982) (table 5). For *Mytilus edulis*, the physiological costs of feeding represents 24 % of the ingested ration (Bayne and Scullard, 1977) whereas digestion and assimilation can be performed after filtration for only 4.6 % of the value of the ingested ration. Oxygen consumption in *Choromytilus meridionalis* is not influenced by ration level (Griffiths, 1980), *Mytilus edulis* has been shown to maintain a constant metabolic rate up to concentration of 280 mg seston.l^{-1} by increasing the percentage of extraction efficiency to 25 %. This increasing of oxygen efficiency consumption balance the decreasing of ventilatory rate (Widdows et al., 1979). In *Crassostrea gigas*, metabolic rates are affected by the ration up to a threshold in food concentration for feeding, over this threshold routine rate remains constant (Fiala Medioni and Copello, 1985). Widdows (1985) shows that mussels subjected to a fluctuating salinity regime maintained a relative constant rate of respiration and feeding between 30 and 20 $\%_0$. Below 19 $\%_0$ there is partial valve closure, feeding cease and respiration is reduced (fig. 21). But there is no acclimation to the fluctuating

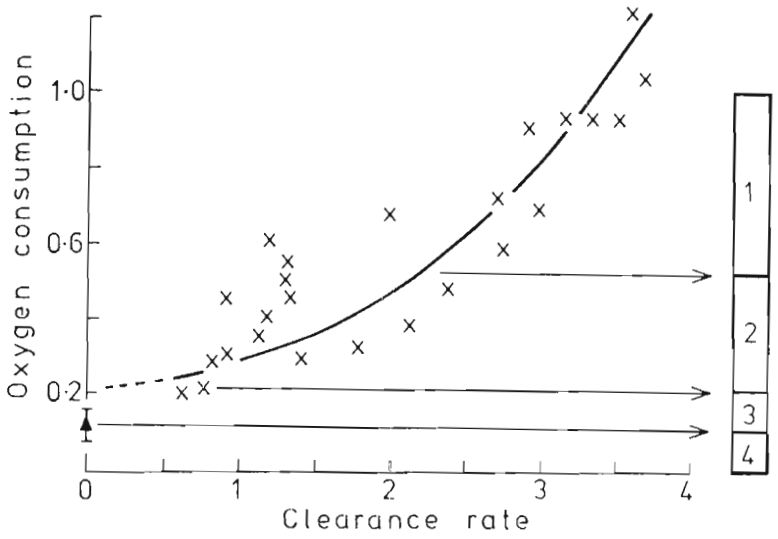

Figure 20 : A relationship between the rate of oxygen consumption (ml O_2 h^{-1}) and clearance rate (l h^{-1}) for *Mytilus californianus* (from Bayne et al., 1975). 1 : Net energy gain. 2 : Costs associated with feeding. 3 : Costs of digestion. 4 : Basal metabolic costs. (from Bayne, 1985).

Table 5 : *Mytilus edulis*. Respiration rate (12°C) in relation to body and size different metabolic conditions (Values calculated from regression equations) (from Navarro and Winter, 1982).

Body size		Oxygen consumption			Energy used in routine metabolism (= 100%)						
Dry-tissue weight	Shell length	Stand. metab.	Stand. metab. + digestion	Stand. metab. + digestion + feeding (= rout. metab.)	Stand. metab.		Feeding		Digestion		Rout. metab.
(mg)	(mm)	($ml \cdot h^{-1}$)	($ml \cdot h^{-1}$)	($ml \cdot h^{-1}$)	($cal \cdot h^{-1}$)	(%)	($cal \cdot h^{-1}$)	(%)	($cal \cdot h^{-1}$)	(%)	($cal \cdot h^{-1}$)
20	13.3	0.0137	0.0196	0.0202	0.0651	67.81	0.0029	3.02	0.0280	29.17	0.0960
50	18.4	0.0274	0.0383	0.0398	0.1302	68.85	0.0071	3.75	0.0518	27.39	0.1891
250	32.6	0.0931	0.1240	0.1308	0.4422	71.17	0.0323	5.20	0.1468	23.63	0.6213
500	41.7	0.1577	0.2056	0.2185	0.7491	72.17	0.0613	5.91	0.2275	21.92	1.0379
1 000	53.4	0.2670	0.3410	0.3650	1.2683	73.15	0.1140	6.58	0.3515	20.27	1.7338
1 500	61.6	0.3634	0.4585	0.4927	1.7262	73.76	0.1625	6.94	0.4517	19.30	2.3403
2 000	68.2	0.4522	0.5656	0.6096	2.1480	74.18	0.2090	7.22	0.5387	18.60	2.8956
2 500	71.8	0.5357	0.6657	0.7191	2.5446	74.50	0.2537	7.43	0.6175	18.08	3.4157
3 000	78.8	0.6154	0.7604	0.8229	2.9232	74.79	0.2969	7.60	0.6888	17.62	3.9088

Table 6 : Nitrogenous excretory products of some bivalve molluscs (from Bayne et al., 1976).

Species	Excreted components as % of total measured nitrogen (N)				Authority
	NH_4-N	Urea-N	amino-N	uric acid-N	
Modiolus demissus	62–75	0	25–38	—	Lum & Hammen (1964)
	66	0	34	—	Hammen (1968)
Crassostrea virginica	65	13	5	—	Hammen *et al.* (1966)
	68	8	21	3	Hammen (1968)
Mercenaria mercenaria	66	0	30	4	Hammen (1968)
Solemya velum	70	0	27	3	Hammen (1968)
Donax variabilis	75	0	24	1	Hammen (1968)
Tagellus plebius	50	0	31	19	Hammen (1968)
Mya arenaria	94	6	—	—	Allen & Garrett (1971*b*)
Mytilus edulis	41	4	55	—	Bayne (1973*a*): winter
Mytilus edulis	67	5	28	—	Bayne (1973*a*): summer

—, signifies that this component was not measured.

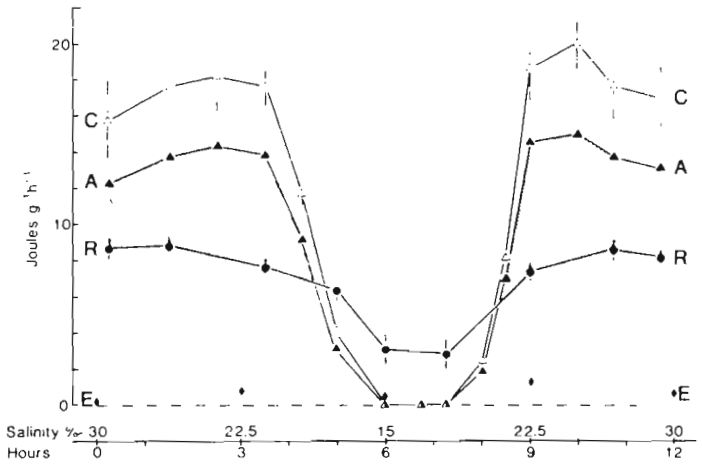

Figure 21 : Effect of fluctuating salinity between 30 and 15 ‰ on the food energy consumed (C, open triangles), energy absorbed (A, closed triangle), energy respired (R, closed circles) and the energy excreted (E, diamonds) by *Mytilus edulis*. Scope for growth (A - (R+E)) is represented by the shaded area (from Widdows, 1985).

salinity regime over 21 days. The metabolic expenditure of marine filter feeders responds also to change in oxygen tension (Newell et al., 1977 ; Bayne and Livingstone, 1977 ; Shumway and Koehn, 1982) and aerial exposure (Widdows et al., 1979b ; Griffiths, 1981). In such case anaerobic metabolism can replace aerial metabolism (see De Zwann, 1977 for bibliographie review ; Widdows et al., 1979b, Ahmad and Chaplin, 1979 ; De vooys, 1979 - 1980 ; Kluytmans et al., 1980). Bayne and Newell (1983), Famme et al. (1981) and Shick et al. (1983) have etablised both by direct and indirect calorimetry (Hammen, 1979) that processes of anaerobic metabolism may account for less than 5 % of total heat loss by *Mytilus edulis* under normoxic conditions. At reimmersion, after exposure to air, *Mytilus edulis* show a typical "oxygen debs" (fig. 22) (Widdowds et al., 1979b ; De Vooys and De Zwann, 1979 ; Shick and Widdows, 1981). Estimations of metabolism losses by oxygen consumption are correlates quite closely with energy requirements as assessed through direct calorimetry for *Mya arenaria* and *Crassostrea virginica*. But for *Mytilus edulis* oxygen consumption measurements could underestimate energy requirements by about 40 % (Hammen, 1979). Furthermore, oxygen consumption is not a relevant measure of energy metabolism during periods of anoxia such as the ones caused by tidal fluctuations.

3.2.3. Excretory losses

This parameter of the energy balance is often ignored, or just estimated by substraction.

As in *Mytilus edulis* (Bayne and Scullard, 1977 ; Bayne et al., 1979 ; Bayne and Newell, 1983 ; Hawkins et al., 1985) *Crassostrea gigas* and *Ruditapes philippinarum* shows seasonal variations in both the rates of nitrogen excretion and the ration between ammonia and organic nitrogen as amino acids or urea (Robert and Vincendeau, 1985). This seasonal variation can be related to changes in the biological conditions (gametogenic for exemple) of the animals and in the level and nature of endogenous energy reserves (Mann and Glomb, 1978 ; Bayne and Newell, 1983 ; Riva and Masse, 1985).

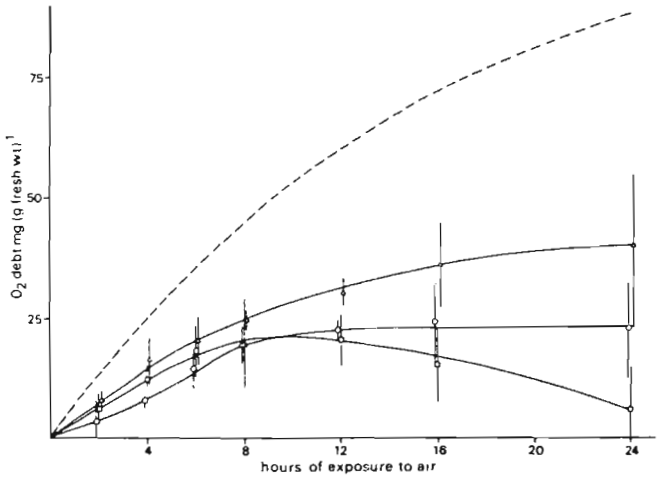

Figure 22 : The extra oxygen uptake (oxygen debt) after re-immersion in seawater, as a function of the duration of the preceding exposure period to air. △ sub-littoral, 45-65 mm ; ○ littoral, 30-50 mm ; □ littoral, 45-65 mm. Values plotted are means ± standard deviation. The dashed curve represents the calculated oxygen equivalent at complete oxidation of the accumulated succinate plus propionate as a function of the exposure time in sub-littoral mussels with a length of 45-65 mm (after data from Kluytmans and de Zwaan, 1976 and Kluytmans et al., 1977, 1978). (from De Vooys and de Zwaan, 1978).

Table 6 shows that ammonia is the main excretory product of bivalvia (Bayne et al., 1976). But in *Mytilus edulis*, the excretion of amino acids accounts for 0 to 63 % of total nitrogen (Bayne and Scullard, 1977). For *Crassostrea gigas*, Robert et al. (1982) show that during summer the urea represents from 30 to 80 % of total nitrogen excretion. Robert and Vincendeau (1985) have measured the seasonal variation in all the components of nitrogen excretion for *Crassostrea gigas* and *Ruditapes philippinarum* (table 7). During summer the excretion rate are highest than during winter, but starvation produces an increase in nitrogen excretion in winter and a fall in summer (Bayne and Scullard, 1977), because the proportional contribution of protein to total catabolism substrats is considerably higher during winter (33 to 67 %) than during summer (6 to 19 %) (Hawkins et al., 1985).

The contribution of ammonia excretion to energy losses in the energy budget may normally be between 1 and 10 % for *Mytilus edulis* (Bayne and Newell, 1983). Thompson (1984a) measured higher ammoniac excretion in non estuarine subartic mussels (17 to 32 % of respiratory energy loss) than Bayne and Widdows (1978) for a lynher population (1 to 12 % of respiratory energy loss), and Srna and Baggley (1976) and Robert and Vincendeau (1985) show an higher excretion for clams *(Mercenaria mercenaria, Ruditapes philippinarum)* than for oysters *(Crassostrea virginica, Crassostrea gigas)*.

As for oxygen consumption, a debt existes for ammonia excretion after tidal exposure to air (De Vooys and De Zwaan, 1978) (fig. 23). This ammonia debt may refleet the ammonia release into the mantle cavity fluid during exposure (Bayne et al., 1976) and/or may be caused by an active deamination of the end product of anaerobic metabolism.

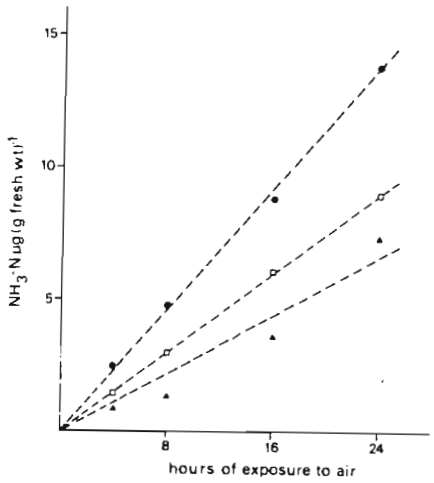

Figure 23 : The extra ammonia excretion after re-immersion in seawater as a function of the duration of the preceding exposure period to air, littoral, 30-50 mm ; sub-littoral 45-65 mm ; littoral 45-65 mm. (from De Vooys and De Zwaan, 1978).

Table 7 : Seasonal excretory product by *Crassostrea gigas* and *Ruditapes philippinarum* (from Robert and Vincendeau, 1985) in uatg/g of dry weight/hour.

Crassostrea gigas		December	February	April	June	August	October
$N.NH_4$	%	12	8.1	28.8	85.4	8.8	73.7
Urea	%	15.5	91.8	19.2	4.7	9.7	26.2
Amino acids	%	-	-	51.9	5.2	6.2	-
unidentified	%	72.4	-	-	4.5	85.3	-
Total nitrogen $\mu gat.g^{-1}.h^{-1}$		6.46	2.32	2.48	2.10	2.36	0.86

Ruditapes philippinarum		December	February	April	June	August	October
$N.NH_4$	%	48.5	1.2	5.2	100	57.2	61.2
Urea	%	3.3	-	8.2	-	6.9	38.8
Amino acids	%	-	-	0.8	-	22.7	-
unidentified	%	48.2	98.8	85.7	-	-	-
Total nitrogen $\mu gat.g^{-1}.h^{-1}$		1.58	16.15	10.92	6.36	2.06	1.51

Conclusion

As it has been said before, two complementary approach of the energy balance are possible. The first, ecological one concerns the resource allocation between productions (Pg. Pr. Ps. Pe.) of natural or cultivated populations, and their seasonal variations. The second, physiological one defines by experimental studies the main causes of variability in the physiological processes of production.

First, the analysis of energy allocation between the secretory products, somatic growth and reproduction related with body size and age is fundamental, but not always easy. If the assessment of energy allocation for *Crassostrea gigas*, *Ruditapes philippinarum*, *Chlamys varia* etc... between somatic growth and reproduction is not really difficult, for *Mytilus edulis*, *Crepidula fornicata* etc..., the diffuse reproductive organs and/or successive and partial spawnings can induce, an underestimation of the reproductive effort. In the same way, natural biodeposition has to be assessed in relation to quantity and nature of potentially used seston by molluscs. By such approach, it will be possible to estimate not only the energy which is consumed, ingested and absorbed on the field (by separation and analyse of feces and pseudofeces), but also the impact of molluscs on the fixed food which can be either resuspended and reused, or can reduce the sediment under the cultures.

Secondly, as Bayne and Newell (1985) argue, the extrapolation of laboratory studies to the field may induce many problems. Environmental and trophic conditions of experimental studies rarely reproduce natural variabilities on the field . In addition of the stress due to acclimation and handling, the results obtained with organisms starved or feed with monospecific phytoplankton culture can induce unsuitable data for environmental studies. Therefore now, the need for more experimental work under natural, field conditions is well recognized, particularly in situations for intertidal molluscs as changeable as in an estuary.

Assessment of actual metabolic losses, especially for tidal molluscs which present an anaerobic metabolism during exposure to air, should be approached by direct calorimetric measures to complement the studies on oxygen consumption. Furthermore, some components of the energy budget are rarely estimated. Mucus produces by gastropods, for locomotion or feeding, can reach more than 30 per cent of the consumed energy. But there is no available assessment for mucus production of filter feeders. A part of this mucus production is ingested with filtred particles, but an other one is lost with pseudofeces production. The losses due to excretion are often ignored or estimated only with ammoniacal products, during laboratory experiments. To assess the magnitude of this potential error in the energy budget, the nature and the seasonal amounts of the all nitrogenous end products must be known. But filter feeders feed not only on particulate food as we have seen, but also on carbonate and nitrogenous dissolved substances. In energy budget nothing is known about the total intake of dissolved substances which, as amino acids, can be either used or excreted by filter feeders.

In the near future if we want to deal with the integrated studies of a shell fish ecosystem and its modelisation it is mandatory to study allto-gether the biochemical, physiological and dynamical parameter not only for individuals but also for populations level as well as the quantity and nature of potential food consumed by molluscs.

Furthermore, a knoweldge of seasonality of energy budgets could allow a better understanding of organisms tolerance and sensitivity to external stresses such as illness or main-induced pollutants.

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DEVELOPMENT OF SHELLFISH PRODUCTION MODELS

C. BACHER *

Résumé :

La modélisation mathématique de processus biologiques est présentée comme un ensemble d'outils de recherche développés en fonction d'un but précis : étude d'impact, bilan énergétique, validation d'hypothèses.

Son utilisation doit être précédée d'une réflexion sur les mécanismes mis en jeu, selon que l'on s'intéresse à un écosystème ou un individu (échelle biologique), que des phénomènes physiques sont pris en compte (échelle physique), à une échelle de temps donnée. Il ne saurait alors exister de méthode générale d'analyse tant sont variées les conditions d'étude, mais quelques cas types permettent d'illustrer la démarche du modélisateur et les récents progrès de ses outils.

Abstract :

Mathematical models for biological processes are presented as a set of tools for research, which have been created for specific tasks : impact studies, energy budget, test of hypothesis.

Before using it, the mecanisms involved must be analysed, depending upon wether a whole ecosystem or one animal is studied (biological scale), physical conditions are taken into account (physical scale), with a predetermined scale for time. The no general method for analysis can be, as conditions of studies are so different, but some typical cases can show the approach of the modelizer and the recent developments of its tools.

* IFREMER, Mus de Loup, BP 133, 17390 **La Tremblade**, France

I. INTRODUCTION

The first definition we could give to model is quite general : a model is any representation of the real world or what it is supposed to be at a given moment ; it clearly depends on the knowledge about reality or part of it ; as an abstraction it is necessary based on concepts and assumptions.

This paper deals with mathematical models only and among them, those which try to stimulate biological mechanisms (for about 15 years however, other mathematical approaches have been developping such as adaptative strategies, adapted from economics). Simulation allows to study dynamical behaviour of the elements of the ecosystem (which we denoted the real world) defined by the modeler. Then two main purposes may be reached by the model :

1) prediction and management of the evolution of the ecosystem,
2) test of the validity of our knowledge and hypothesis

Consequently model needs both mathematical and biological information.

A classification of the different kinds of models is proposed by Levins (quoted by Wiegert, 1979) according to three criterions : precision, realism and generality, one of these being generally inconsistent with the two others. For instance a realistic and precise representation of a given ecosystem will be probably unvaluable for another one. On the contrary, a general and realistic model will provide qualitative clues about the mechanism studied and poor information for prediction. Nowadays most of (classical) models aim at being general and precise ; common examples are Lotka-Volterra equations (inter- and intraspecies competition) or Von Bertalanffy's growth curve.

Whatever the case, the conception of the model consists in the same few steps. The first step is the definition of the compartements and relationship among them (Wiegert, 1975) ; compartments represent amounts of mass or energy (variables) within trophic levels or foodweb elements (when the model depicts an ecosystem) ; relationships describe the mass or energy flows whereby the variables will change. Forcing functions may be included ; for instance the laws of temperature and light are know, to influence the phytoplankton growth ; a waste water input may bring organic and detritic material. Thus the complexity of the model depends on two factors ; number of compartments (Wiegert, 1975) ; knowledge about interactions and the way to describe them in mathematical equations.

Evolution of all the compartments will be translated into differential equations. The frame work is thus established.

The parameters are usually provided by experimental or field data. Some of them may be evaluated so that the model results fit the data (optimization). This stage is called calibration.

Once the rationale defined, the acute problem is in fact the validity of the model, coupled to its utilization as a tool for more investigation. The validation consists in comparing the data and the model curves and looking for good agreement. Statistics are rarely employed though classical tests are used by Rice (1984) to evaluate the proportion of the mean square error (MSE) explained by the model.

A sensitivity analysis is often conducted ; here the goal is the study of the model responses to the variation of some parameters values ; such an approach is really useful ; for instance Warwick (1977) tested hypothetical trophic relationship through simulations run with different values of the diet parameters in one compartment. Some models are conceived to study impact of

disturbances ; Menesguen (unpub) uses a phytoplankton zooplankton model to measure the impact of thermic disturbances created by power plant.

We shall see that models are run with a wide range of issues. Before dealing with production model, I would like to give some information about several kinds of models used either to simulate filtration mechanism or to analyse energy flows.

The former may be integrated in general production model as a submodel. The latter is powerful as soon as the circuit of energy is emphasized. This review also shows that the mathematical description of the process (filtration, growth, production) must be consistent with the different scales involved : time, spatial and biological scale ; a monthly growth will not be depicted by the same equations as a daily one since short term phenomenons shall be erased in the former case ; spatial variability can be integrated when the patchine of the ecosystem is too important (Wiegert, 1975) ; the world of the ecosystem is generally based on trophic levels or foodweb elements ; the biological scale is then defined from the lumping of species.

II. FILTRATION, ASSIMILATION

1) Lehman (1976) tries to predict the filter feeder behaviour at both low and hign food concentration thanks to an energy optimization assessment. The filter feeder aims at maximizing the quantity $Q = E_A - E_F$, where E_A is the net gain from assimilation and E_F the loss due to the filtration expense. The basic equations enables the author to take various diets into account. Denoting the filtration rate F and the density of particles i, D_i E_A equals $\sum E_i D_i F$ where E_i is the net energy gain from digestion of a particle ; E_F is supposed to be a power function of F, $E_F = aF^b$, F is related to the gut volume, the number of ingested particles of each type, the volume and calorific value of these particles as a function of the time spent inside the gut. Moreover an active or passive selective ingestion is added to the model.

This theoretical view of the filtration activity is lowered by the lack of data (Taghon and al., 1978) about such parameters as gut passage time and assimilation efficiency (it is one of the numerous problems the modeler has to face with). However, the first conclusions drawn from the model are consistent with the observations found in the litterature, even if the validity is not proved ; assumption on selectivity and assimilation may be tested by this model which, as its author says, can be used to guide experiments. Goldstein (1971) compares two compartimental models of ingestion and assimilation for fish ; very simple, these predictive models may be extrapolated to other species but more data are needed in order to calibrate and test the parameters which define the kinetics between the compartments. (FIG 1)

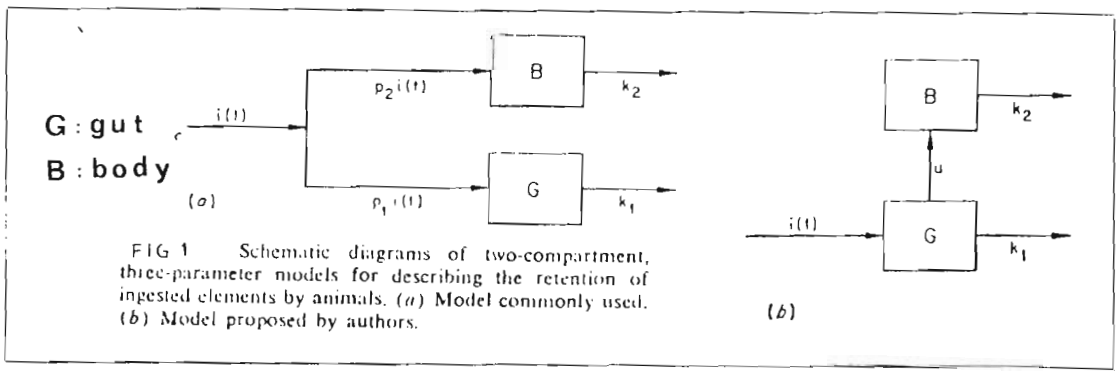


FIG 1 Schematic diagrams of two-compartment, three-parameter models for describing the retention of ingested elements by animals. (*a*) Model commonly used. (*b*) Model proposed by authors.

Another descriptive and predictive model is shown by Slagstad (1981), who depicts the dynamics of gut in copepods with hypothesis on assimilation and diets ; the volume of an ingested cell decreases at a constant digestion rate and the assimilation rate is stated to be proportional to the undigested fraction of cells inside the gut ; the digestion rate and the minimum gut passage time are supposed to control the assimilation efficiency. (FIG. 2)

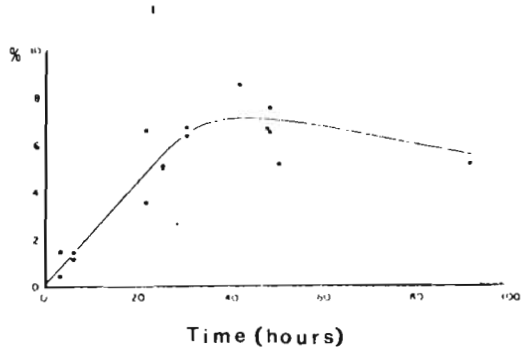


FIG. 2 Percentage of ingested ^{137}Cs in the body compartment, *B*, of 10 g bluegills (*Lepomis macrochirus*) after fish were fed a single meal of *Chironomus* sp. larvae labeled with ^{137}Cs (modified from Kolehmainen and Nelson 1969)

The previous models are somewhat theorical and suffer from the paucity of data ; they show that writing mathematical equations may improve one's knowledge about complex mechanisms. The following models are perhaps more classic, as numerous available measurements make calibration possible.

2) Majkowski (1980) has developed an energetic model on the Rotifer Brachionus rubens, on the basis of the wellknown energy budget equation C = P + R = A (faeces are not taken into account) his purposes are :

1) to understand the dynamics of energy flows through the animal
2) to lead comprehensive studies to improve the knowledge about production.

Consequently, such a model should be useful in an ecosystem simulation. The fundamental equations are written :

$$C = C_1 (\emptyset)\ W^{C_2} \quad \text{(allometric relation)}$$

$\emptyset$ = food concentration

$$C_1 (\emptyset) = a\ (1 - k\ e^{-b\emptyset}) \quad \text{(Ivlev relation)}$$

(limitant effect of the food)

$$U = \frac{A}{C} = u_1 + \frac{u_2}{C_1 (\emptyset)} \quad \text{assimilation efficiency}$$

inversely proportional to C_1

$$R = r_1\ W^{r_2}$$

$$r_1 = r_3 + r_4\ f^{r_5} \qquad \text{with } f = \frac{C_1 (\emptyset)}{\emptyset}$$

(f is the filtration rate, in volume X time $^{-1}$)

A reproduction term is also expressed as a function of $\emptyset$ and including life span and age at maturity. Then the evolution of the total calorific value of the body is simulated. (FIG. 3)

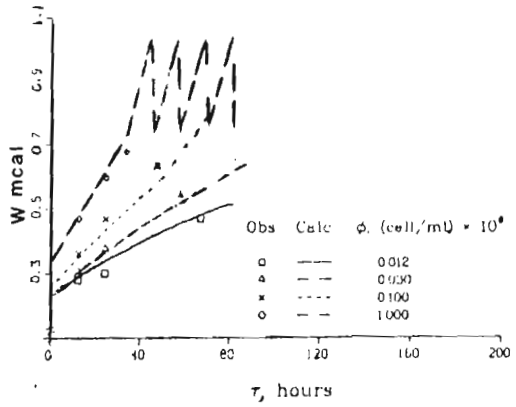


FIG. 3 Relation between the body calorific value of the male rotifer, W, and its age, τ, at various constant food concentrations, ϕ.

The validity of the model is stated for low concentrations since the simulation fits the data quite well-goodness of fit is also seen on C, A, P, R versus Ø curves. The sensitivity analysis of this model allows the author to indicate which parameters are important and must be precisely measured (food consumption, respiration and assimilation efficiency). One may wonder whether such a model cannot be applied to molluscs.

Another model designed by Bayne (1976) relates the same mechanisms in a different manner, to food concentration, body weight and temperature. The rationale is logical and corresponds with the widespread hypothesis on filtration. The model excludes pseudofeces and emphasizes the filtration of particles without selection ; dissolved dubstances assimilation and recycling problems are dropped :

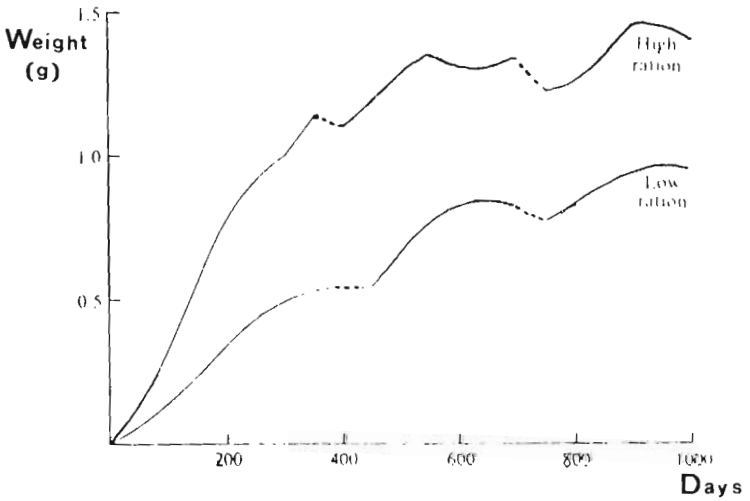


FIG. 4 The growth of *Mytilus edulis* over 1000 days at 'high' and at 'low' ration, as determined by a simulation model. The dashed portions of the curves signify weight loss due to spawning.

$f = aW^b$ filtration rate (volume X time^{-1})

Only a fraction of the material brought by the filtration is ingested ; the rate of ingestion is a fonction of W (body weight) and Ø, food concentration. Bayne computed it as a decreasing fonction of Ø, then Ø is greater than a threshold value ; for Ø less than $Ø_o$ the rate of ingestion equals 1 ; as Ø increases the rate reaches an asymptotic value.

This material is partially assimilated ; the assimilation efficiency depends on body weight, temperature and the weight of organic matter intake R. Respiration is an allometric expression ; it varies with temperature and R. An other allometric relation is given for fecundity, though few data are available.

These series of equations are quite general for bivalves ; based on regressions, they should be precise ; they depict the energy flows through the individual according to the balance :

$$C = R + F + P_g + P_s, \text{ so that}$$
$$P_s = C - R - F - P_g \qquad \text{(FIG. 4)}$$

A subroutine predicts the variations of the nitrogen contained in the body. As Majkowski's, the model is said to be predictive and useful fo pointing out misunderstanding. For instance everybody will not agree Bayne's equation of the pseudofeces (Widdows, 1979). Nevertheless hisfundamentals are admitted by Verhagen (1982) in his population model.

The flaws of models most often correspond with the lack of available data on important biological problems. Thus recycling pseudofeces egestion or dissolved matter impact on filtration are often disregarded. The models may test ideas about these phenomenons provided that data exist. These hypothesis stated from simulations are about to start experiments.

3) This review of individual short term models would be incomplete without an example of the kinetics approach which will lead to further developments. Amouroux (1982) studies the interaction between the Venus Verrucosa, dissolved matter, particulate matter faces, CO_2 and bacteria compartments in a closed system. He finds good agreement between

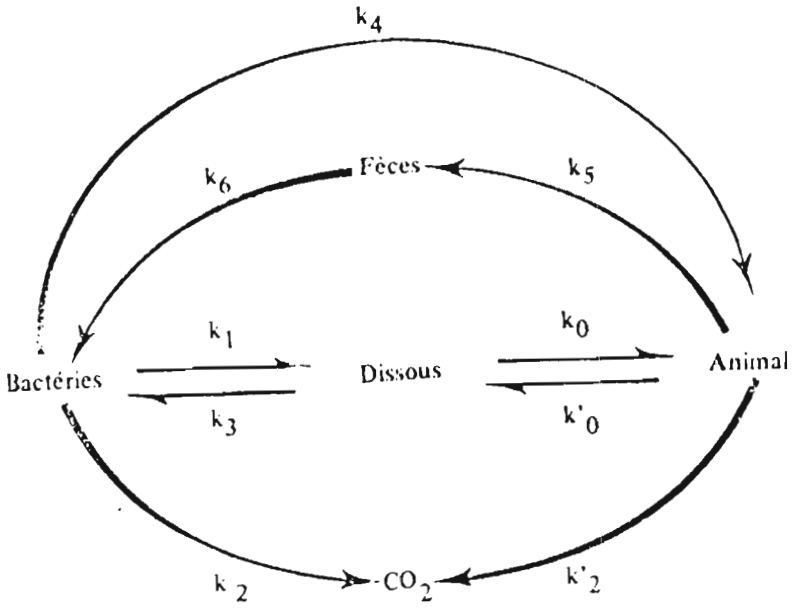


FIG. 5 Flows between compartments

his data and simulation curves on short term experiments (40 hours). Differential equations are assessed to be linear (first order kinetics) and the parameters are evaluated from different submodels results. Amouroux showed that bacteria are quickly consumed and feces are recycled.(FIG.5)

III. ECOSYSTEM

The ecosystem modeling must avoid the danger and the temptation to gather numerous submodels which increases the complexity, the non stability of the model and thus fails in producing adequate simulations (Patten, 1975), though the model seems realistic (Park, 1975). The application of individual and short term growth or filtration model to huge ecosystems doesn't make sense, since the time scale and the number of species integrated are quite different.

Furthermore a complex hydrological structure may interfere with biological mechanism. The movement of particles is derived from physical transport equations, usually solved by numerical calculations.

1) Physics

Denoting - X a particle concentration, the equation of evolution is written :

$$\frac{\delta X}{\delta t} + \vec{V} \nabla X = \nabla . K \nabla X + \text{sinks} + \text{source}$$

(Chahuneau, 1980)

$X = X(t, x, y, z)$ where x, y, z are spatial coordinates

$\vec{V} = (V_x, V_y, V_z)$ current speed

$\nabla X = \left(\frac{\partial X}{\partial x}, \frac{\partial X}{\partial y}, \frac{\partial X}{\partial z}\right)$ divergence operator

diffusion matrix $K = \begin{pmatrix} K_x & 0 & 0 \\ 0 & K_y & 0 \\ 0 & 0 & K_z \end{pmatrix}$

$\vec{U} . \nabla X$ represents the advection, which is the part of the transport due to the current speed.

$\nabla . K \nabla X$ equals the diffusion term caused by variations of X concentration. This equation is usually integrated on the vertical dimension (z) ; thereby we obtain a similar equation with new terms representing the wind effect and the friction on the bottom (boundary constraints) ; sinks and sources sum up the whole biological interactions wich influence X concentration, and physical forces (sedimentation, Coriolis) coupling the physical and biological submodel allows to classify models according to the complexity degree: number of spatial dimensions and number of trophic levels or foodwebs elements
(Chahuneau and al., 1980).

Both physical and biological parameters have to be estimated and the sampling must include the spatial variability in order to keep validation possible. The physical complexity level is connected to the temporal scale and the purpose of the whole model ; a phytoplankton biomass model for a lake will generally refer to seasonal changes ; di Toro (1975) elaborates a rather simple phytoplankton model in a lake divided in seven spatial elements (boxes) ; c_{ij} is the concentration of substance i in segment j :

$$V_j \frac{dC_{ij}}{dt} = \sum Q_{kj} C_{ik} + \sum E'_{kj} (C_{ik} - C_{ij}) + \sum S_{ijk}$$

where V_j is the segment volume,
Q_{kj} the net advective flow rate between k and j
E_{kj} the bulk rate of transport, fonction of the difference of concentration between

i and a, adjacent segment. These segments are defined from homogenous regions in which advection and mixing flows are measured.

The model simulates the nitrogen and phosphorus circuit through phytoplankton, zooplankton benthic compartments with classical phenomenons : grazing mortality excretion, regeneration from organic to inorganic forms, primary production temperature and light are the (classical) forcing fonctions. The model is neither precise nor realistic but may give information on the evolution of eutrophication with increasing human population.(TAB. 1)

ILLUSTRATIVE APPLICATION OF THE EUTROPHICATION MODEL [a]

Year	Observed [c]	Population accelerated growth [d]	Population moderate growth [d]	Population limited growth [d]	Two foot Lake-level change [d]	Phosphorus removal (50% agriculture)	Phosphorus removal (95% + detergent)	80% P [b]
1930	15 μg liter^{-1}	—	—	—	—	—	—	—
1970	25 μg liter^{-1}	—	—		Δ2 μg/liter [e]	Δ1 to 2 μg liter^{-1}	—	—
1990	—	37 μg liter^{-1}	30 μg liter^{-1}	—	—	—	10–15μg/liter [c]	15 μg liter^{-1}
2010	—	42 μg liter^{-1}	35 μg liter^{-1}	26 μg liter^{-1} 28 μg liter^{-1}	—	—	15–20μg/liter [c]	20 μg liter^{-1}

a The information presented should be considered an illustration of the types of results obtainable from application of eutrophication models to analysis of planning problems rather than a projection of future conditions.
b These levels are for the moderate growth population levels.
c The same algae levels can be obtained with an 80% phosphate removal policy plus 1990—25% nitrogen removal and 2010—50% nitrogen removal.
d Values are micrograms/liter of chlorophyll for Western Lake Erie in Section 7 of the eutrophication model (near the Maumee River).
e Change in chlorophyll levels from 1970 conditions.

TAB. 1
Effect of population growth, agricultural land use policy or lake-level change on eutrophication.

Beside management purpose, population dynamics may be outlined. For instance, Verhagen (1982) elaborates a coupled biological and physical model about a mussel population evolution. The fundamentals of the biological submodel are derived from Bayne's (1976) to which larval development equations are added. The water circulation is driven by the wind speed and the bottom geography, so that the salt lake may be divided in nearly closed volume elements. Field data show that these elements correspond with the musselbeds and can then be considered as independent boxes. Inside a box, measurements show that the physical transport may be reduced to a vertical dispersion and a constant horizontal advection ; denoting C (z,t) the particular matter concentration at depth z and time t, we have :

$$\frac{\partial C}{\partial t}(z,t) = u(C_o - C) + D_z \frac{\partial^2 C}{\partial z^2}$$

= advection + vertical diffusion (FIG. 6)

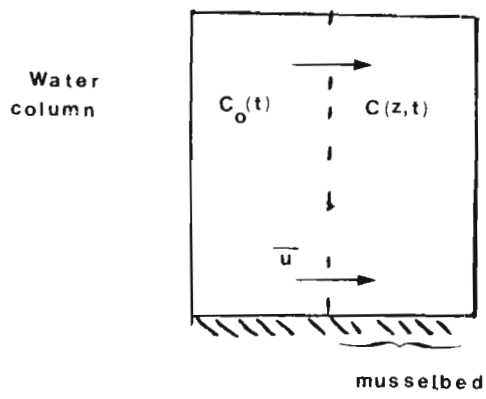


FIG. 6 Structure of the water column above a musselbed (see text)

The integration of this equation provides the amount of available food at the bottom, where the mussels lie. Regarding then the biological model, the ratio of ingestion rate par m^2 per day is estimated and allows to conclude that the primary production is almost completely consumed by the mussels. Short-comings are revealed by the comparison between calculated and extrapoladed cohort evolution (FIG. 7)

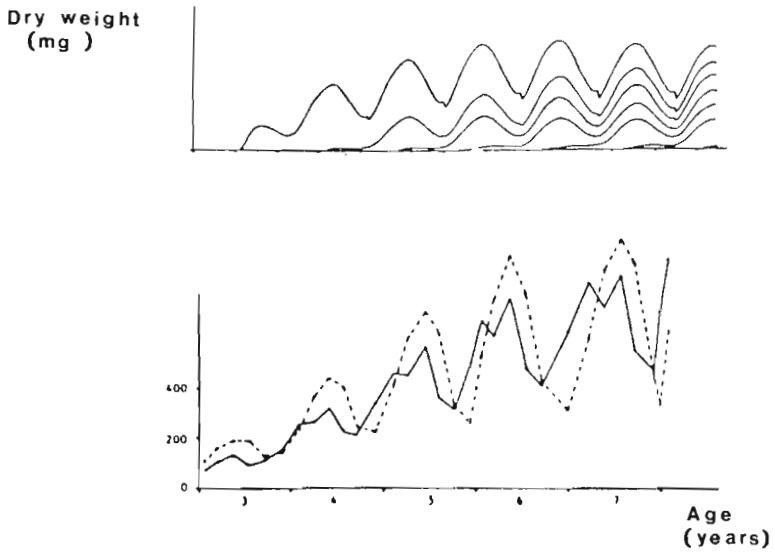


FIG.7--Growth in weight of calculated cohorts compared with measured data from Bayne and Worrall (1980).

However simulations show the same trends as the observed curves. Verhagen outlines the lack of available data about cohort analysis ; this is an acute problem, modelin are often faced with. Another problem consists in interpretating the mathematical properties of the models provided by the non-linearity structure ; for instance Verhagen finds a good agreement between long term predicted oscillations and observed ones ; but it does not seem reasonable to take into account the long term conclusions of a model previously built to study annual events. Nevertheless, providedthat temporal scale, spatial scale and the rationale are kept in mind, modelisation gives relevant results.

2) Ecosystem analysis

The generalization froman individual to a whole population approach is meaningful when a few species are regarded. As soon as a global ecosystem is studied, such a description seems inadequate, for too many non-lineary mechanisms are integrated so that the mathematical properties of the system (stability, periodicity) are not controlled (Patten, 1975). Realism may be integrated at a reasonable degree ; Wiegert (1975-77 and 79) improves the linear transfer equations by using threshold effects to describe limitant phenomenons. Matter or energy flow from compartment i to j is written :

$$F_{ij} = t_{ij}\, x_j\, f(x_i, x_j) \qquad 0 \leq f(x_i, x_j) \leq 1$$

f (X_i, X_j) is explicited through the (realistic) definition of two kinds of competition, exploitative and interference competitions which may be separated ; the former is the competition for material resource, the latter the competition for space. Then thresholds are included ; ingestion increases from a saturation to a

refuge level under or upper which the ingestion rate equals zero or one ; between these two values, the ingestion rate is supposed to be a linear function of the resource. Applied to a six compartment ecosystem, the model predicts the evolution of some compartments quite well and then is used to predict the impact of a perturbation on one compartment (Wiegert, 1977). According to Wiegert, his rational proves to be general, precise and realistic.

Quite linear systems are also elaborated. They are valuable in so far as the ecosystem is in steady state (dynamical equilibrium). Under normal conditions, they may fit the observed evolution data but most often provide smooth evolution curves, due to the averaged parameter values and mainly temperature forced interactions.

They first aim at test biological hypothesis and emphasize the energy pathway bewteen the foodweb elements (groups of species showing the same feeding behaviour). Warwick (1977), for instance, has built a six-compartment model to simulate the production of the secondary producers ; as other models, the equations are based on main conservation and include respiration, mortality secretion and ingestion, activities ; the parameters are derived from the litterature or from field data ; species are lumped in homogenous compartments (FIG. 8)

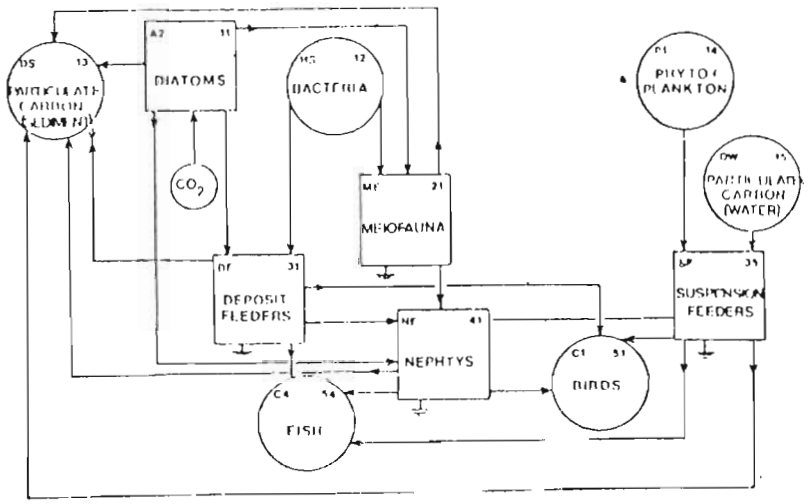
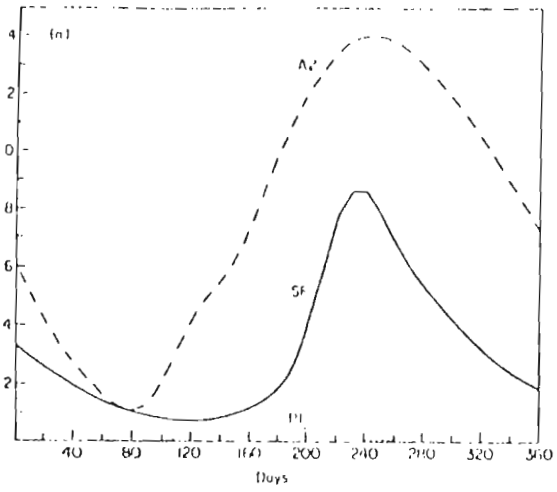


FIG. 8 Carbon flow in Warwick's model

resulting from the foodweb structure (biological scale). Simulations give information on the tendancy of the carbon flow during the year. Though not precise, the order of magnitude seem valid. Furthermore biological assessments are tested such as the effect of different diets on the growth of Nephtys. (FIG. 9)



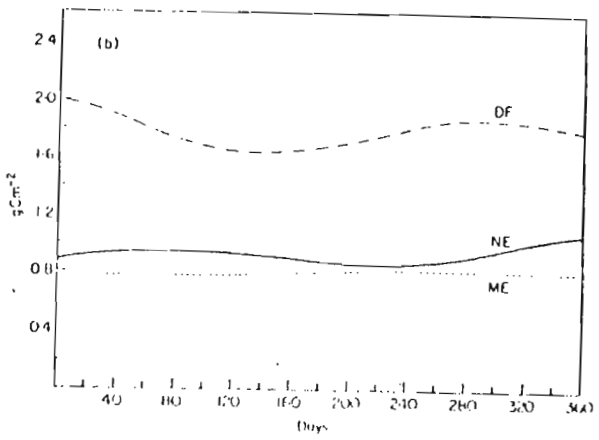


FIG. 9 The results of the dynamic simulation model; (*a*) for phytobenthos (– – – A2), suspension feeders (SF) and the values of phytoplankton (···· PI) supplied as an exogenous variable and (*b*) for meiofauna (··· ME), deposit feeders (– DF) and *Nephtys* (NE). (*c*) the results of a simulation where *Nephtys* fed only on meiofauna and deposit feeders and not on phytobenthos and (*d*) where *Nephtys* fed exclusively on phytobenthos, and not on meiofauna or deposit feeders.

Analysis of such linear systems is developed by Hippe (1983) and Hannon (1973) who use matrix calculation to investigate the properties of the flow circuit through the ecosystem. The general mass conservation equation is written :

$$\dot{x}_i(t) = z_i(t) + \sum f_{ij}(t) - \sum f_{ji}(t) - y_i(t)$$

x_i is the amount of energy in compartment i and $\dot{x}_i = \frac{dx_i}{dt}$ the rate of change.

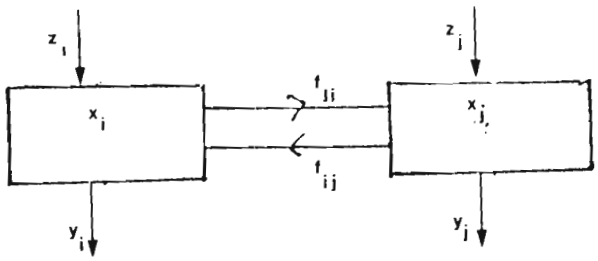


FIG. 10 Flow circuit in a quite general compartment model (see text)

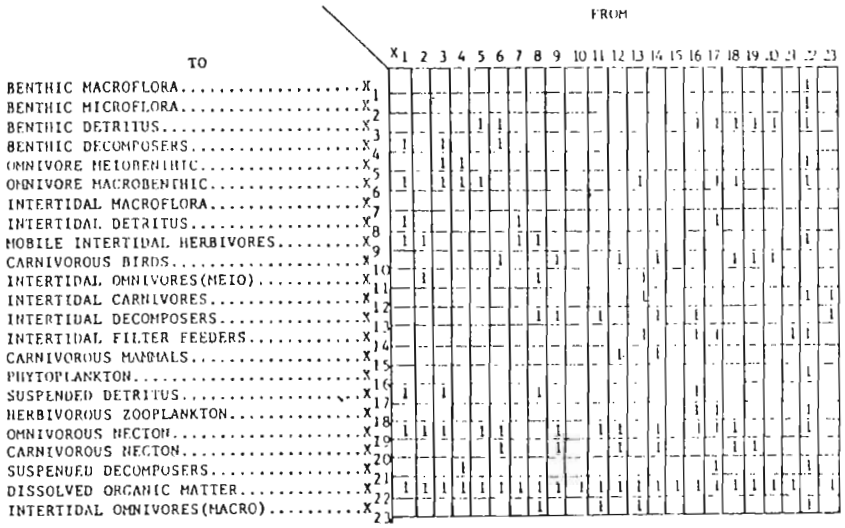
y_i represents the output outside the system from i, and z_i the input toward i, f_{ij} is the flow relating j to i. Hippe defines the through flow T_k as the amount of energy which passes through the compartment k, supposing that in a steady state ($s_{ik} = 0$) inflow equals outflow ; in the dynamical case

$$T_k(t) = \sum f_{kj}(t) + z_k(t) - x_k = \sum f_{jk}(t) + y_k(t)$$

The basic hypothesis of the model is that the flow f_{ij} from j to i equals a fraction q_{ij} (t) of the flow through i (donor controlled interaction). Matrix calculation enables the author to write then $(T_1 \ldots T_n) = (Y_1 \ldots Y_n)\ (I - Q)^{-1}$

I is the identity matrix and Q = (qij), $(I - Q)^{-1}$ = (aij) then the relation fij = qij Ti may be written fij = $\sum_k (q_{ij} a_{ki}) y_k = \sum_k f_{ij}^k y_k$,

Thus f_{ij}^k is the value of fij when y_k = 1 and $y_{k'}$ = 0 for k' ≠ k, Consequently it represents the intercompartmental flow between j and i, contributing to one unit of outflow y_i (t). Hannon (1973) points out that this approach shows the "energy flow interdependence of each species upon the other" ; it reveals the structure of the ecosystem, eluded in the classical differential equations such as predator-prey ones. System analysis completes the realistic and precise modelisation. Dame (1977, 1981) has applied this procedure to a marsh - estuarine system ; the equations of his models are linear and involve 23 compartments that can be clumped in three submodels. The complexity of the biological structure is shown by a relation matrix displaying the interrelationships between all the compartments.(TAB. 2)



TAB. 2 The relation matrix for the total North Inlet model. A positive relation is noted with a 1

The ecosystem reaches a steady-state level consistent with the observed stability. Energy flow analysis is conducted through a six-compartment sub-model.(FIG. 11)

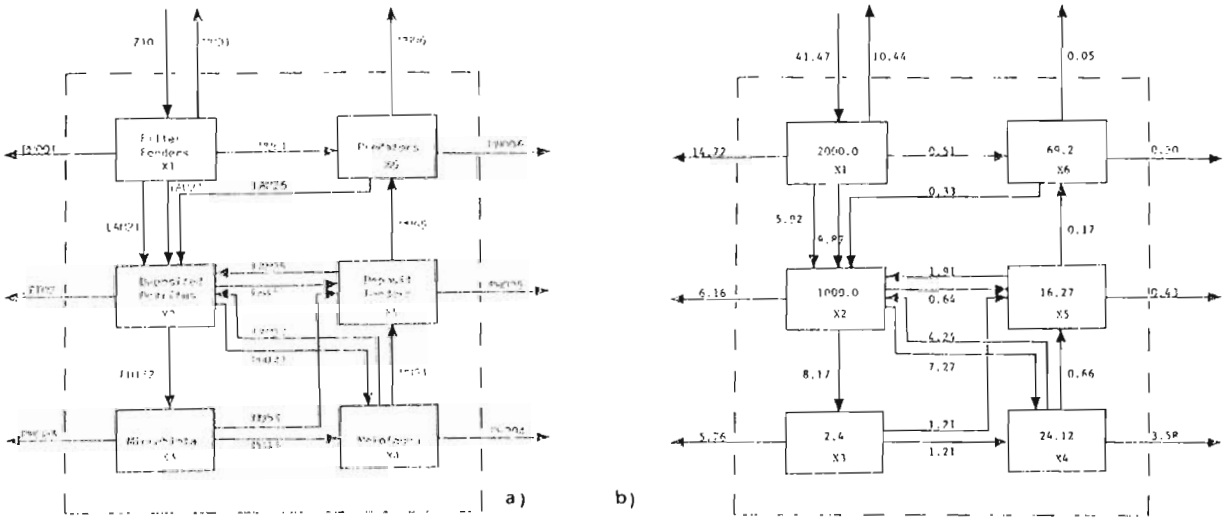


FIG. 11 a numbers associated with each symbol denote a to/from relationship; for example, M1061 indicates mortality by predators X6 on filter feeders X1 or a flow to X6 from X1

b Energy flows (Kcal m^{-2} d^{-1}) and standing crops (Kcal m^{-2}) in an intertidal oyster reef

Throughflows are examined for different imput and ouput vectors. The average pathlenght of an inflow (AP LZ) is the number of compartments crossed by a given imput. Energy cycling can be estimated through the efficiency $RE = \frac{Tii-1}{Tii}$ when Tii represents the flow through i (see table 3)

Measure	State					
	Filter feeders (X1)	Detritus (X2)	Microbiota (X3)	Meiofauna (X4)	Deposit feeders (X5)	Predators (X6)
Throughflow (Ti)	41.47	22.27	8.17	8.48	2.51	0.69
Average pathlength of a unit input (APLZ)	2.02	2.59	1.84	2.54	3.12	2.23
Average pathlength of a unit output (APLY)	1.00	2.93	3.93	4.07	4.71	2.93
% Total system throughflow-inflow	100.00	–	–	–	–	–
% Total system throughflow-outflow	30.10	21.66	27.10	17.45	2.43	1.26
Recycling efficieney (RE)	0.00	0.28	0.09	0.23	0.11	0.01

Total system throughflow (TST) = 83.58; Total system throughflow straight (TSTs) = 74.33; Total system throughflow cycled (TSTc) = 9.21; Average pathlength (APL) = 2.02; Average pathlength straight (APLs) = 1.79; Average pathlength cycled (APLc) = 0.22; Cycling index (TSTc/TST=CI) = 0.11

TAB.3 Computation of throughflows, pathlengths and recycling

Thereby structural properties of the ecosystem are outlined and reveal the main flows.

IV. MARENNES-OLERON ESTUARY

A) We have reviewed some examples of model applied to population biomass evolution ; here, population defines a species or a part of the ecosystem ; production is the difference between the outflows and the inflows from or to the population. The wide range of patterns we have seen deserves to be introduced for it gives some idea on recent development of modelisation. To sum up this investigation, the consistency of the model depends on :

1) The structure of the ecosystem : exogenous fonctions, time and spatial scales, number of compartments and relation matrix have to be examined.

2) The purpose of the simulation : prediction, management, or trophic relations study

3) The rationale of the model : linear or non linear equations, coupled physical - biological interactions, thresholds

4) The available data

Among the tools that can be used to draw conclusions from the simulation, the most powerful are : systems analysis, sensitivity analysis, disturbance effect, validation, tests of hypothesis.

Generally speaking, the complexity of the model must be slowly increased. It is a wise rule which should avoid uncontrolled simulated behaviours.

Goal \ Scale	Temporal scale	Spatial scale	Biological scale
Prediction	1	0 - 1	0 - 1
Energy flow study	1	0	1
Mecanism	0	0	0
Interrelationship	0 - 1	0 - 1	0 - 1

TAB_4 0 : short term, uncoupled physics or individual level

1 : long term, coupled { physics / biology } or { food web / trophic levels }

B) We are trying to modelize the Marennes-Oleron estuary in order to study the interaction between the growth of oysters and the available food.

Environmental conditions may be outlined as following :

1) Short term physical transport of particles occur ; the water flow is staying for about 10 days in the estuary and this residual movement is an average of all the tidal fluctuations.

2) The whole oyster population reaches about 80 000 tons ; the mussel biomass is given to be 5 000 tons ; beside these cultured population, wild species are to be estimated but they probably are negligible competitors.

3) A phytoplankton bloom is observed in April or May in the North of the estuary ; during the year successive detritic (in winter) or living matter (in summer) inflows take place ; these materials are brought to the oysters by the residual movement, from North toward South.

A high turbidity prevents the primary production from occuring in the major part of the estuary ; the high concentration of non biotic particles probably lowers the oysters ingestion efficiency ; moreover little information exists about the rejected part of food (pseudofeces).

The model will aim at high-lighting the limitant effect of food on oyster growth ; in a first stage, the estuary may be compared to a raceway with boundary constraints (food current) and a forcing fonction (temperature) Because of the environmental conditions the time scale is about three months (March, April, May). The second step should study the growth - decreasing food relationship more precisely thanks to a coupled physical - biological model. The physical model has already been achieved ; it computes the water level and the streamline at about 1000 points of a grid ; it has to be adapted to foresee the particle pathway through the estuary during a tidal cycle (14 days).

Some data are or will be soon available ; the dispersion of oysters, primary production, growth as a fonction of the tide and the geographical place, filtration parameters and the water composition. However lack of information on gametogenesis and food recycling must be pointed out.

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MANAGEMENT OF EXPLOITATIONS IN COASTAL AREAS

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AMENAGEMENT DES EXPLOITATIONS DANS L'ESPACE COTIER

SUMMARY OF SESSION ON MANAGEMENT OF EXPLOITATIONS IN COASTAL AREAS

H. KAN-NO, J.M. GATES

Dr Kan-no began the session by outlining the experiences with shellfish management in Japan.

Dr GATES and Dr MEURIOT outlined their perspectives on the subject matter. Dr. GATES focused on four topics viz (1) estimation of value, (2) allocation mechanisms, (3) properties to be considered in evaluating allocation mechanisms and (4) some reflections on economic development.

Dr MEURIOT stressed two characteristic of shellfish culture, viz (1) the externality in production and (2) the absence of a market mechanism for allocation between alternative uses of space and environment.

Bioeconomic models may take into account externalities ; however, they have first to be backed by sociological or political science studies, analyzing on the one hand the strategies followed by different types of enterprises and, on the other, the rationales of existing institutional processes.

Tokai Regional Fisheries, Research Laboratory, 5-5-1 Kachidoki, Chuo-Ku, **Tokyo** 104, Japon

RÉSUME DE LA SESSION SUR L'AMÉNAGEMENT DES EXPLOITATIONS DANS L'ESPACE CÔTIER

H.KAN-NO, J.M. GATES

Le Dr.KANNO ouvre la séance en présentant les expériences acquises au Japon dans le domaine de l'exploitation des coquillages.

Les Drs. GATES et MEURIOT soulignent leurs vues sur le sujet. Le Dr. GATES insiste sur quatre points 1) l'estimation de la valeur, 2) les mécanismes d'allocation de la ressource, 3) l'intégration de la notion de propriété dans les mécanismes précédents, 4) quelques réflexions sur le développement de l'économie.

Le Dr. MEURIOT met l'accent sur deux caractéristiques de la conchyliculture 1) les externalités de la production et 2) l'absence de mécanismes de marché pour l'allocation, entre différentes utilisations possibles, de l'espace et de l'environnement.

Des modèles bioéconomiques pourraient prendre en compte ces phénomènes externes. Toutefois, il serait utile, tout d'abord, de faire un retour en arrière avec des études sociologiques et politiques qui analyseraient, d'une part, les stratégies suivies par des entreprises de types différents et, d'autre part, la raison des processus institutionnels existants.

* Tokai Regional Fisheries, Research Laboratory, 5-5-1 Kachidoki, Chuo-Ku, **Tokyo** 104, Japon

BIO-ECONOMIC ANALYSIS OF SHELLFISH-CULTURE ACTIVITY IN FRANCE

B. GILLY *, E. MEURIOT *

ABSTRACT

Bio-economic models are not in common use in the field of shellfish culture and may prove to be an important analysis and evaluation tool. This paper will deal only with the potential contribution of these models to furthering knowledge of the dynamics of production and marketing systems. Such models should enable us to determine interactions between the strategies used by the various participants in this field, as well as between the shellfish industry and other areas of economic activity, whether it be at the level of the individual operation, the shellfish basin or the industry. In particular, it can be shown that external factors have an influence on the shellfish industry (for example by determining the relationship between tank load and quantity and value of production), and an evaluation may be made of the economic repercussions of various space allocation and environmental utilization scenarios.

key words: shellfish industry, bio-economic models, external factors, operating strategy, economic analysis

RESUME. Les modèles bio-économiques sont encore peu développés en matière de conchyliculture et peuvent constituer un outil d'analyse et d'évaluation important. Seul l'apport potentiel de tels modèles dans la connaissance de la dynamique des systèmes de production et de commercialisation est discuté ici. Ils permettent en principe d'appréhender les interactions, d'une part, entre les stratégies des différents agents du secteur et, d'autre part, entre le secteur conchylicole et les autres activités économiques, dans les entreprises, des bassins conchylicoles et la branche d'activité. Il est possible, en particulier, de montrer les externalités affectant la conchyliculture (par exemple en dégageant les relations entre la charge d'un bassin et la production en quantité et en valeur) et d'évaluer les répercussions économiques de scenarios alternatifs d'allocation de l'espace ou d'utilisation du milieu.

mots-clés : conchyliculture, modèles bio-économiques, externalités, stratégie d'exploitation, analyse économique.

* Département Stratégies de Développement et d'Aménagement,
Institut Français de Recherche pour l'Exploitation de la Mer, 44039 **Nantes** Cedex, France

INTRODUCTION

Culture of shellfish in France is basically being done in small-scale facilities, often as family operations. There are a number of similarities between shellfish-culture and certain forms of agriculture: work is mainly performed by family members, supplemented where necessary by a small number of permanent employees and a larger number of seasonal employees, and the future of the operation is normally dependent on the manager of the facility. Above all, shellfish-culture activities, like agriculture, require the permanent use of a given space, and production levels are partially dependent on the area under culture.

Shellfish-culture activities nevertheless differ from agriculture in several ways, and we shall discuss two of these:

- production levels in a shellfish-culture operation do not only depend on the surface farmed and the means of production used. They are also dependent both on total basin load and on water quality, that is, in both cases, on decisions made by other operators or users of the space. These interdependencies, which affect the production of each operator, make up what economists call "external factors".

  These external factors in the shellfish-producing industry are related to those that exist in the fishing industry: the production of a fishing vessel depends in part on the total fishing effort applied to

List of abbreviations used:

CCM	Commissions des Cultures Marines (marine culture commissions)
CIAT	Comité Interministériel d'Aménagement du Territoire (interministerial committee on national development)
COREP	Commissaire de la République
DASS	Direction Actions Sanitaires and Sociales (sanitary and social action branch)
DDE	Direction Départementale de l'Equipment (departmental equipment branch)
ENIM	Etablissement National des Invalides de la Marine (national association of naval veterans)
MSA	Mutualité Sociale Agricole (agricultural social benefit association)
POS	Plans d'Occupation des Sols (land use plans)
SAUM	Schéma d'Aménagement et d'Utilisation de la Mer (program for development and use of the sea)
SDAU	Schéma Directeur d'Aménagement and d'Urbanisme (master plan for urbanism and development)
SMVM	Schéma de Mise en Valeur de la Mer (maritime development plan)
SNDCA	Schéma National Directeur de la Conchyliculture et de l'Aquaculture (réservation des sites) (national master plan for the shellfish and aquaculture industry - site reservations)

a fish stock. They differ by the fact that, in the fishing industry, some operators may increase their fishing capacity and make a profit, to the detriment of other operators, while in the shellfish industry, all operators in a given basin share the consequences of pollution or epizootic disease: there are only losers.

- allocation of operating space is not done, in France, on the basis of acquisitions or the location of private property.[1] These areas are part of state-owned maritime lands. They are not allocated by a free market process; rather, allocation is governed by regulations.[2] Granting of concessions on state-owned maritime lands is the responsibility of a state official, the Commissaire de la République, for the region involved, acting on recommendations from a "Commission des Cultures Marines" (CCM) including representatives from the administration, parliament and professional groups. Development of activities that will interact with the shellfish industry or compete with it for use of space and the environment, may be furthered or hindered by other decision-making centres such as municipalities, general and regional counsels and various administrative bodies.

1. ECONOMIC ANALYSIS

Economic analysis may play a three-fold role:

(i) contribute to better knowledge of the structure and dynamics of production and marketing systems, since economic analysis is aimed at producing explanatory outlines that are meant to represent causal interdependencies,

(ii) clarify future actions, that is, to forecast the economic consequences of some decision that is currently being envisaged,

(iii) contribute to defining the process of allocating resources in fields where the free market does not come into play.

Only the potential contribution of bio-economic models to knowledge of the dynamics of production and marketing systems will be discussed here.

The causal interdependencies to be studied in analysing the shellfish industry have to do with:

(i) the shellfish industry itself, actions by individuals and enterprises (individual strategies), relations between production zones and within a given basin (collective strategies),

(ii) relations between this sector and other competitive or complementary economic activities.

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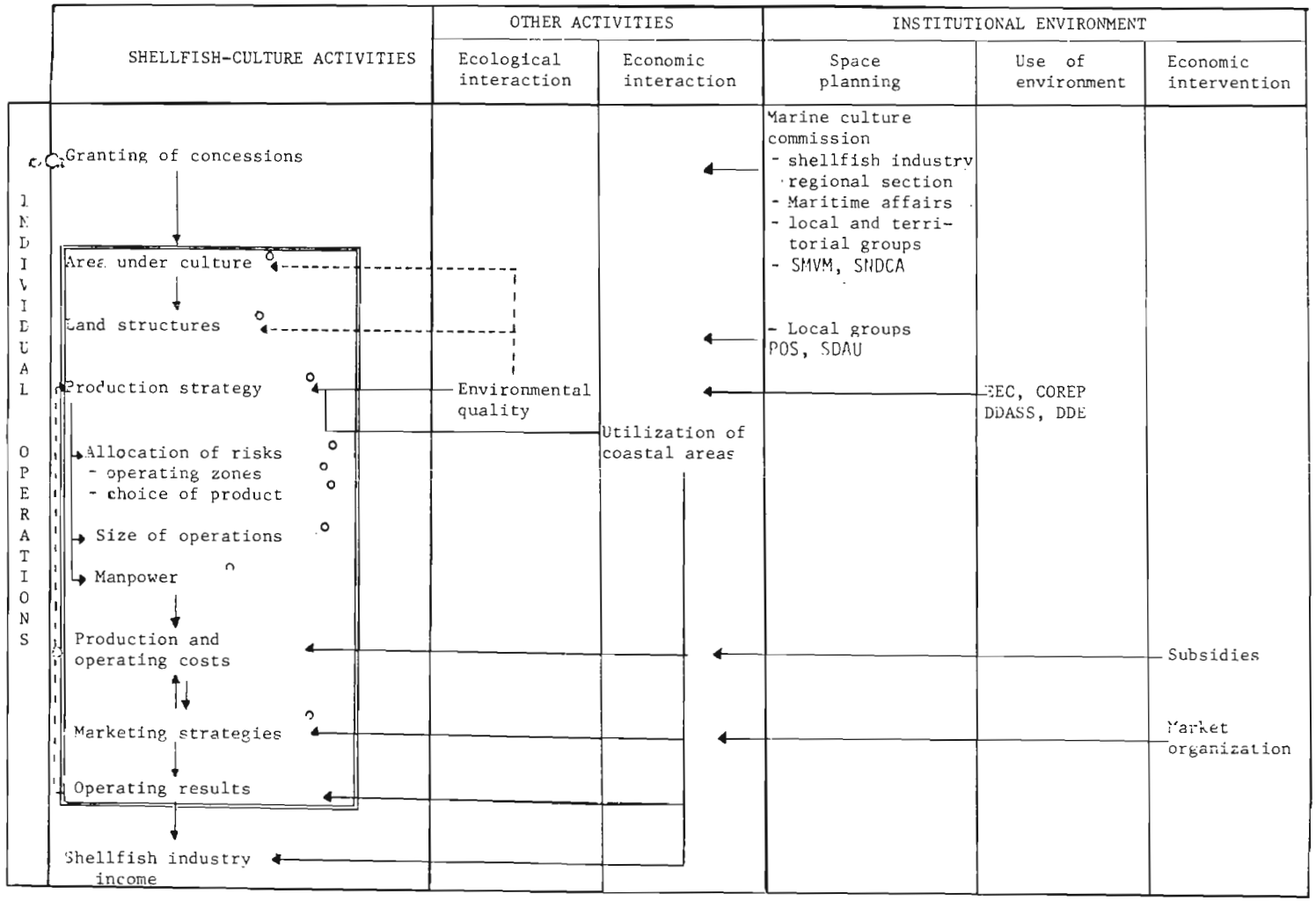
[1] With the exception of land installations, which may be privately owned.

[2] Décret No. 83-228, 22 March 1983, laying down the regulations governing authorization of marine culture operations.

TABLE 1: INTERACTIONS AND ENVIRONMENT: INDIVIDUAL OPERATIONS



It is possible to break these interactions down into three aggregate levels: individual operations (individuals or enterprises), shellfish-culture basins, and the sector as a whole. At each of these levels, inter-dependencies cannot be understood outside the social and institutional context in which they occur (Table 1).

1.1 Individual operations

The results of a shellfish-culture operation depend on its choice of operating strategy. These choices will have an effect on its income and on the make-up of its production and/or operating costs, for example:

- choice of product, collection of spat and/or nursery culture and/or maturation,
- allocation of risk, distribution of concessions over several producing basins. This distribution may lead to specialization of production, which is a function of costs,
- choice of marketing strategy: among oyster-farmers, for example, there are both producers and shippers,
- choice of size of operation: use of family labour alone or hiring of permanent or seasonal employees.

Each shellfish-culture operation develops its own strategy on the basis of the limited information it has in order to attain its own objectives. Each producer does not necessarily react on the basis of all the inter-dependencies listed above, since most of the time the information he has deals only with prices and working time.

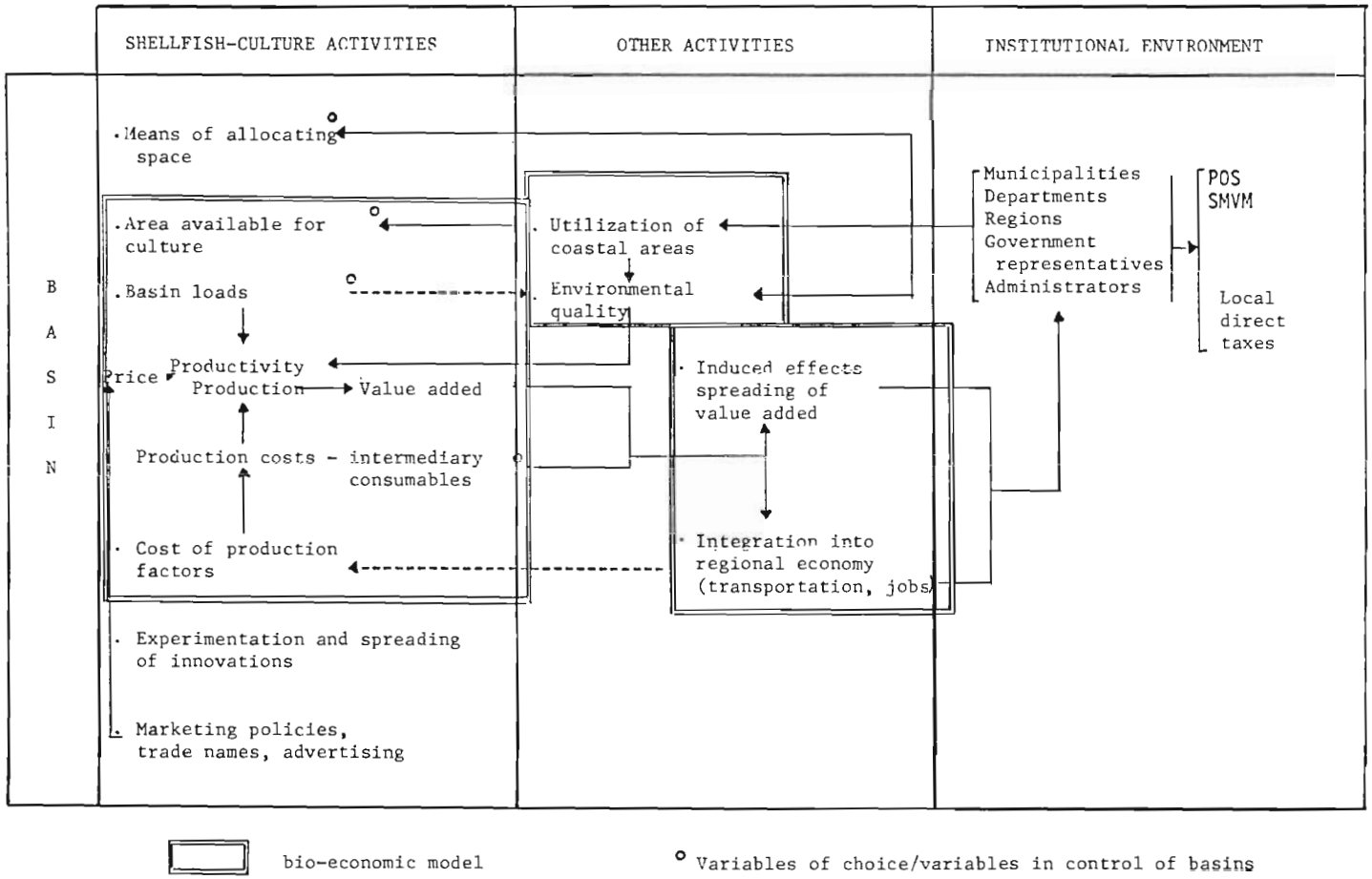
Entering the field (and leaving it), as well as individual development strategies, involves land-tenure problems. The way in which shellfish concessions are managed reduces the degree of freedom enterprises have in developing their own strategies: marine culture commissions often feel it is best to take back a concession that is not used at at least 50% of its capacity. In the same way, the lack of systematic renewal of expiring concessions may be a disruptive factor.[1]

The influence of other economic activities being carried on in the same area as the shellfish operation may be felt in various ways:

- existence of activities that complement shellfish-culture, such as agriculture, fishing or tourism, may make it possible:
  1) for the operator to exercise another activity, and thus to have other sources of income (fisherman/shellfish-farmer, for example)
  2) to have seasonal labour available to the shellfish industry.
- on the other hand, the existence of permanent activities that are less demanding or more profitable may deprive shellfish farmers of the man-power reserves they require.

[1] Payeur, F. (1984).

TABLE 2: INTERACTIONS AND ENVIRONMENT: SHELLFISH BASINS



Economic analysis of shellfish-farming operations is a new field, and while bio-economic models have been developed in some countries (in particular in the U.S.A.), they are non-existent in France. Bio-economic models, at this level of aggregation, are built without explaining external factors; variations in the various parameters are considered to be exogenous, no matter what their origin. The purpose of these models is to establish relations between the various inputs and their costs and the value of production. The bio-economic models thus constructed have two main functions:

(i) pedagogical function, by showing the parameters and variables that enter into the composition of an individual result: what interactions there are between areas farmed, choice of product, size of enterprises, production costs, cost of intermediate consumables, etc. and the results obtained by shellfish-culture operations,

(ii) these models may also be used to evaluate the sensitivity of results to variations in the relative importance of various parameters, making it possible to *guide* decision-making in such areas as:

- choice of individual strategies (influence, *ceteris paribus*, of a variation in spat price, collected vs hatchery vs imported spat),

- orientation of certain aspects of research (influence of a variation in shellfish growth rates on operating results).

The role of the models is not to determine optimum production conditions for an enterprise representative of the sector and to compare the results of each operation to the model. It is more to the point to attempt to establish a typology of shellfish-farming operations, not only based on traditional criteria (area, tonnage produced), but also on the strategies adopted (production scales, allocation of risks, manpower, growth). This typology could be based on two types of criteria:

- total or partial completion of a culture cycle. This may result from a natural constraint (e.g. impossibility of collection north of the Loire) or from a deliberate choice pinpointing the existence of markets at various stages in the culture process. Based on strategical choices such as spat producer and/or culturer and/or finisher-shipper, Dumont (1) was able to distinguish 19 categories of operations.

- production structures. These are many and varied: capital invested, manpower employed, number of activities exercised by operator, etc., and at the present time are difficult to quantify.

The models thus developed would make it possible to test, for each type of operation, their sensitivity to the results of variations in parameters and then to compare these sensitivities for the various types of operations in a given environment.

1.2 Basin

Total production and value added in a shellfish basin, as well as operator income, are related to the area under culture and production per unit of area.

[1] Dumont, P. (1983)

The *area available for shellfish culture*, as well as the possibilities for land installations are the result of decisions taken at the institutional level[1] with respect to use of coastal areas. To a great extent, these decisions are an exogenous variable for shellfish operators. They may influence the decision-making process through pressure from their professional association and the economic arguments this organization may present. The stakes are quite large: development of the shellfish industry is partly through the creation of concessions outside areas already being used, and the development of other, competitive activities, in terms of space or use of the environment, may be nearly irreversible. For municipalities, the shellfish industry is often poorly situated in comparison with other activities due to the absence of tax income, since there are exemptions both from business taxes and property taxes on developed properties.[2]

The strategies of various shellfish-industry groups may act directly through *the criteria chosen for the use of available space*. Shellfish-industry organizations may propose a local policy for operating structures.[3] Officials (Commissaires de la République) will thus be led to adopt regulations, after consultation with marine culture commissions, on the minimum and maximum dimensions of new concessions granted. The means for applying for vacant concessions and allocation of these concessions play an important role, due to the possibility for encouraging or preventing certain types of activity. For example, proposals put forward recently by professional groups for defining the minimum area for installations in a basin might favourize applicants over 35 years of age, to the detriment of younger applicants.[4]

Biological production models make it possible to take into consideration external factors due to the effect of basin loading on carrying capacity or the impact of other ecological variables in the environemnt. Bio-economic models may enable the results obtained by biological shellfish production models to be translated into terms of costs and income. These bio-economic models may be confined to interactions between the production factors used, basin loading and production, with unit costs and prices being considered exogenous. They may be integrated into larger models that trace the integration of the shellfish industry into the regional economy as well as induced effects through spreading of value added through the economy.[5] These models make it possible to consider the following aspects:

- potential for seasonal employment or supplementary income; costs, such as transportation, which depend on the regional economic climate,

- an overall increase in shellfish-culture activity would bring with it an increase in consumption of intermediate goods and in purchases of equipment; suppliers of goods and services would see an increase in their activities, which would lead to a rise in their purchases.

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[1] Land-use plan (P.O.S.), developed at the municipal level. Maritime development program (S.M.V.M.) prepared by the State and assigning authority to the various municipalities and regions and to the State.

[2] Prat, J.L. (1983)

[3] Décret No. 83-228, 22 March 1983, laying down regulations governing authorization of marine culture operations (Art. 4).

[4] Payeur, F. (1984)

[5] Harris, C.C. and Norton, V.J. (1979)

- an increase in value added in the shellfish industry causes a rise in total wages and salaries to employees and operations; the effects of this increase may cause a chain reaction through expenditures by employees and operations in other sectors of activity.

These studies of the effects of variations in final demand on regional economies have been used, for example, to calculate the economic consequences of pollution caused by the grounding of the Amoco Cadiz.[1]

1.3 The shellfish sector

Interrelations between the various shellfish operations may occur on a national level, through the existence of a professional organization and training structure, and through processes for determining prices (markets) and costs.

(i) Professional organization: Based on a system close to that of fisheries[2], the shellfish industry is characterized by the weakness of its union representation and the absence of a local structure, like that of the local maritime fisheries committees, in individual basins. There are six regional sections, which together form an interprofessional shellfish industry committee, which is in term represented in the CCPM.

(ii) Training is provided by maritime trades schools and by specialized vocational high schools.

(iii) Overall influence of the national (and international) economic climate on the shellfish industry as a whole depends on several factors (Table 3).

- Production costs: The cost of a number of consumables is beyond the control of producers, e.g. cost of hatchery or imported spat, cost of equipment such as sorters which partly depend on the existence of industries using similar techniques, manpower costs (ENIM - MSA).

- Investment: Financing mechanisms (subsidies, banking system, interest rates, etc) are crucial factors in investment decisions.

- Industry turnover: the industry has very poor control over demand factors. Producers can only act on consumption through collective advertising and cooperative financing by the State (FIOM) and producers. Other parameters that are just as important are not controlled: available income, foreign trade, constitution of reserves, etc.

There are very few global economic models in France today. For the time being, there is no model of supply (make-up of costs)[3], and very few models of market functioning. One example that might be mentioned is that prepared by P. Dumont (1983) for the cupped oyster. This study shows, first, that there is great variability in the demand for cupped oysters compared to retail prices (1:11) and disposable income (1:01). Second, these considerations and the low value of consumer price elasticity compared to operating costs show that marketing and distribution structures in France do not always coincide with domestic supply.

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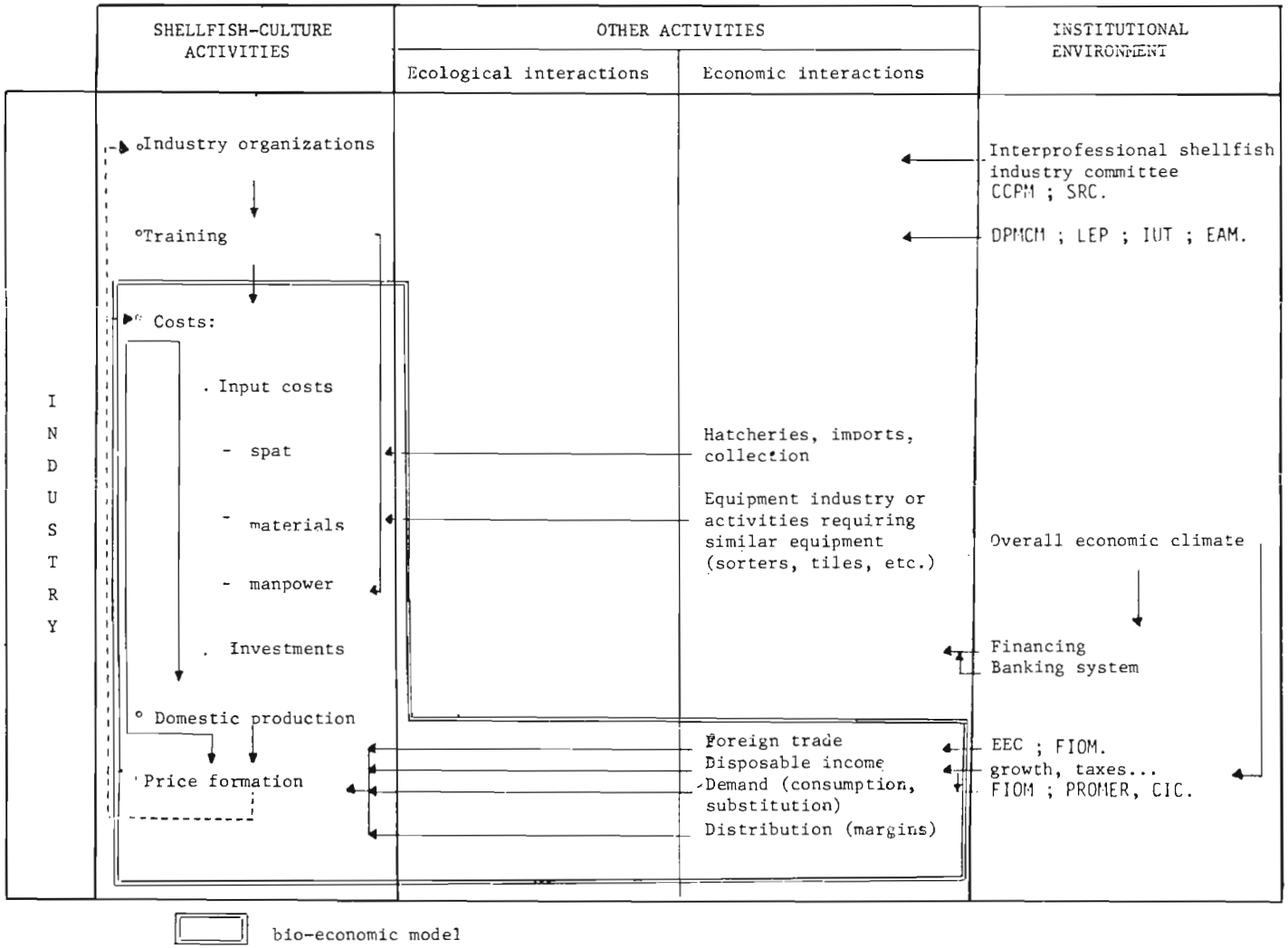
[1] Bonnieux et al. (1980

[2] 1945 Ordinance; Décret of 17.02.1958, amended in 1968.

[3] cf. Dumont, P. in preparation.

TABLE 3: INTERACTIONS AND ENVIRONMENT: SHELLFISH INDUSTRY



CONCLUSION

Bio-economic models may form an important analysis and evaluation tool. In principle, they make it possible to determine external factors affecting shellfish-culture activities, for example, by showing the relationship between basin loads and quantity and value of production. They may also be used to evaluate the economic repercussions of alternatives for space allocation or use of the environment.

The potential for developing accurate models and using them as an aid to decision-making is nevertheless uncertain in France:

- Practical difficulties involved in obtaining reliable information on shellfish operations may jeopardize the possibility of developing bio-economic models in the very near future, especially since:

  - biological models of shellfish production have not yet been developed,

  - very few economic studies exist on the shellfish industry, and little is known about the strategies followed by shellfish farmers in areas such as access to space or investment, financing structures, the impact of taxation and other important aspects.

- The potential scope of bio-economic models is related to the manner in which the results of this research are used; however:

  - At the basin level, the results obtained from models may emphasize the interest of a group strategy (for example limiting basin loads). This strategy is nonetheless difficult to reconcile with that currently being followed by some operators, whose profits are related to better production estimates and pricing prospects than those of their competitors. As well, under-estimating production means that some income is concealed from the taxation authorities.

  - Development of coastal areas and of conditions of environmental use is carried out through a consultative process in which pressures inevitably come into play; for example, choice criteria resulting from a cost-benefit type of economic analysis may not be taken into consideration. The situation in France is, from this point of view, different from that encountered in countries such as the United States, where evaluating the economic impact of various decisions on the use of natural resources is a necessary preliminary to decision-making.[1]

It is essential to involve disciplines such as sociology or political science in the study of the crucial elements affecting the dynamics of the shellfish sector of the economy, e.g.:

- knowledge of the choices and strategies available to operators, either as individuals or groups,

- decision-making processes leading to arbitration of conflicts on use of space and the environment, the role and conditons of using scientific information in these decision-making processes.

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[1] Cf. for example the case of the Water Resources Council: "Establishment of Principles and Standards for Planning", Federal Register, Vol. 38, No. 174, September 10, 1973.

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SOME ECONOMIC ASPECTS OF AQUACULTURAL ALLOCATION

J.M. GATES *

SUMMARY

We have reviewed allocation issues with particular focus on estimation of allocation quantity and value, possible allocation mechanisms, and certain properties to consider in designing allocation mechanisms. A recurring theme in the discussion was the existence and tension between the twin goals of economic efficiency and a "good" incidence or distribution of the gains from efficiency. This theme is ubiquitous in economics and, as a result we cannot assert a unique "best" answer to many allocation problems. Quantitative economic analysis can measure the potential gains and describe the distributional implications of alternative policies. The rationale of such measurement and description is that it faciltates more informed decision-making in either the public or private sectors of the economy. Finally, I have sketched briefly some thoughts on the potential role of mariculture and maricultural research in economic development. Scientists in the biological sciences will continue their lead role in generating the new knowledge and technological progress on which development rests. However, other disciplines may become involved since production is but the first link in a food chain extending from estuaries to final consumers.

RESUME

Les différents points concernant l'allocation de la ressource sont présentés, plus particulièrement les voies possibles et certaines caractéristiques à prendre en considération lors de la définition des mécanisme d'allocation. Un sujet est revenu dans la discussion : l'existence des deux objectifs antagonistes que sont l'efficacité économique et l'adéquation des retombées et de la distribution des gains de cette efficacité. Ce thème est ambigu en économie et par conséquent nous ne pouvons pas fournir une réponse optimale unique à beaucoup de problèmes d'allocation de ressources. L'économétrie peut mesurer les gains potentiels et décrire les conséquences sur la distribution des différentespolitiques. La justification de ces évaluations et descriptions est de permettre une prise de décision en meilleure connaissance de cause, aussi bien dans le secteur public que privé. La conclusion présente succintement certaines idées sur le rôle que pourrait jouer l'aquaculture et la recherche (en aquaculture) dans le développement économique. Les biologistes garderont leur rôle de chef de file pour l'acquisition des connaissances et les avancées technologiques sur lequels repose le développement. Cependant, d'autres disciplines devront intervenir car la production n'est que le premier maillon d'une chaîne alimentaire qui va des estuaires jusqu'au consommateur.

* Department of Resource Economics, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A.

It is a pleasure for me to attend this symposium because it has afforded me an opportunity to hear of recent developments in shellfish mariculture. Aquaculture was the focus of my first research on arriving at the University of Rhode Island. Although my more recent research has been in fisheries, I retain an interest in aquaculture and teach a course in aquacultural economics.

I have been asked to address issues of allocation. In so doing I will arrange my remarks around the following four topics:

(1) Estimation of Allocation Quantity and Value
(2) Allocation Mechanisms
(3) Properties to Consider in Designing Allocation Mechanisms
(4) Reflections on Economic Development and Employment Issues

The first topic will illustrate that the quantity allocated and its valuation are intimately related; the information needs are the same for either. The second topic will be a brief description of various allocative mechanisms which have been used in other sectors of many economic systems. The third topic will sketch the possible ranges of each of several important attributes which are shared by some or all of these mechanisms. The fourth topic is a brief outline of how mariculture and economic analyses may contribute to economic development.

ALLOCATION QUANTITY AND VALUE

This topic may be approached analytically with the aid of a simple model. The basic components include an inverse demand function, an aggregate production function, a cost function and an aggregate net benefit function derived from these.

Demand: $P=p(Q)$; P=price
Q=aggregate harvest
and $p'(Q)<0$ by assumption

Production Function:
$Q=q(N)$; N=number of licences or homogeneous firms
and $q'(N) > 0 > q''(N)$

Cost Function:
$C=c(N)$; $c'(N) > 0 > c''(N)$

These specifications are sufficient for our purposes but they are unnecessarily strong.

Benefit Function:

B=Net Benefits=Consumer Benefits minus Production Costs

$$= \int p(Q)dQ - c(N)$$

Under the specifications above, the necessary and sufficient conditions for maximum net benefits are:

$$\frac{\partial B}{\partial N} = P.q'(N) - c'(N) = 0$$

The solution, denoted by $\overset{*}{N}$, is the number of licenses or homogeneous firms which would maximize aggregate net benefits.

Substitution of $\overset{*}{N}$ in the profit function of producers, yields:

$$Q=q(\overset{*}{N})$$

$$\overset{*}{P}=p(\overset{*}{Q})$$

and

$$\text{Profits}=\overset{*}{P}.\overset{*}{Q}-c(\overset{*}{N})>0$$

The unit value of a license is then aggregate profits divided by the

(optimal) number of licenses, $\overset{*}{N}$.

The above is, of course, a gross oversimplification. As such it is rather sterile unless one can find empirical counterparts of the functions presented. This will require both economic work on market determinants and interdisciplinary work from biology, physical oceanography (spatial distribution within an estuary may be as important as N itself) and economics. Undoubtedly, one would wish to enrich the model by making it dynamic and, perhaps more importantly, by making it stochastic. It is noteworthy that at the above generality, a case for public intervention has not been established. It has not been established, because the underlying mechanisms have not been specified. If, for example, one envisions an estuary in which the food supply is a fixed rate, then the curvature of the production function, while regrettable, is not a cause for public intervention. There may be locational rents which accrue to producers whose locations are superior, but the size of the economic pie is maximized via a market solution. Conversely, suppose that food supplies and hence carrying capacity are governed by a set of differential or difference equations. Then it is possible, indeed likely, that decentralized self interest of autonomous producers will result in overstocking and a reduction in the size of the economic pie. The same is true if the outbreak of epizootics is strongly dependent on stock density. Here the mechanism is a density dependent stochastic process. The "health" of the population is an indivisible or public good. For such goods, the market is seriously flawed and some sort of intervention may be desirable. Even here, however, intervention is not neccessarily desirable. It is possible that the costs of intervention exceed any potential gain. If so, epizootics, while regrettable, would be best tolerated rather than trying to eliminate them.

Having had some experience with fisheries problems, it is perhaps worth acknowledging the existence of multiple use conflicts. Such conflicts may appear at times to be the dominant characteristic of fisheries. For our purposes today, however, it seems appropriate to abstract from such issues.

ALLOCATION MECHANISMS

The number of permutations in allocation schemes is considerably reduced if one distinguishes between the mechanism itself and the properties and conditions which may be associated, in varying degrees, with each. The principal mechanisms are territorial rights, fee simple and leasing systems. To this one may append any number of arbitrary mechanisms; a point to which we shall return in due course.

Territorial Rights

Territorial rights have been described for many fisheries by social scientists in the disciplines of sociology and anthropology. From a perspective of economic efficiency, the rationale of allocation is a means to an end; that of increasing the size of the economic pie. The fact that allocation involves explicit or implicit determination of how the economic pie is sliced is secondary to this end. Unfortunately, the work in this area suggests that this perspective is inverted under territorial rights. The process has been shown to have significant effects on how the pie is sliced. In particular, it tends to favor "insiders" or "local" persons and to exclude "outsiders". I am aware, however, of only one empirical work demonstrating at least partial effectiveness of territorial rights. I suspect that the tendency toward excessive entry and the "tragedy of the commons" remains. There may be some transitory, marginal effects on entry.[1] Also, it should not be assumed that territorial rights are costless merely because the public sector is not involved. The individuals involved may be incurring significant but unrecorded costs. Unlike the public sector, however, we can be confident that such costs do not exceed incremental benefits. Despite these reservations, one must acknowledge territorial rights as an n'th best alternative. That is to say, if it is the best that is attainable, it is probably better than nothing. This is especially true since such mechanisms tend to evolve in a policy vacuum.

Fee Simple or "Ownership" Systems

In fee simple systems, the concept of ownership or use rights is (nearly) absolute. These systems correspond to what is usually thought of as "property rights". Although ubiquitous, such systems are only one extreme on a continuum of use right possibilities. The more common situation is one in which individuals have more limited use rights;of which leasing is illustrative. More typically, the owner is proscribed from actions or activities deemed undesirable for one or more reasons.

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[1] See James Wilson, "A test of the tragedy of the Commons," in Garrett Hardin and John Baden (eds.) Managing the Commons (San Francisco: W.H. Freemans Co., 1977), pp. 96-111. This research was well done; whether the results observed are permanent or transitory is not known.

Leasing Systems

In leasing systems, a lessee aquires rights to engage in specified activities for a specified duration of time. Often, some terms of the lease are stated negatively; that is to say, certain activities or practices are proscribed as a condition of the lease. Thus, either leasing or ownership systems may contain restrictions; the primary difference appears to lie in the longevity of use rights. In ownership systems ownership remains with the owner indefinitely unless the owner decides to dispose of the allocation by sale, gift or bequest to other(s).

Under either of the two preceding systems, issues arise in connection with the transfer of rights. Initially, the issue is one of rationing of use rights among competing users. The methods used in market economies have included auctions and "Land Grants". Auctions in competitive markets tend toward an equilibrium at which the seller receives the capitalized value of profits from the operation. Thus, by rationing the quantity to be allocated to a correct level, the allocating agency leaves price determination to market forces. Within auctions, the commonest type is one of "bidding up". The bid price typically starts very low. Each successive bid raises the price until a maximum willingness to pay is reached. The reverse bidding process, sometimes referred to as a "Dutch Clock" method has been tried in marketing cattle. Here the bid starts high and is gradually lowered by the auctioneer. The first person to bid then receives the allocation at the price bid. This system is said to put greater pressure on buyers and to result in higher auction prices. By contrast, a "Land Grant" system takes the pricing process in the opposite direction. This results in excess demand which must be rationed by non-price methods. Typical rationing mechanisms include Land Grants, random processes (lotteries or the draft). In principal, both systems can be equally efficient. They differ in distributional effects. In auctions, the revenues are captured by a central authority in charge of allocation. In a land grant system, the profits of culture remain with the culturist, or at least are subject only to the same types of taxes (income,value added, etc.) as other sectors of the economy.

The final method is one for which a convenient name escapes me. With the forebearance of this audience, I will draw upon a characterization used by a fisherman. The method could then be called the "HEIRS OF RED HAIRED MEN WHO HARVESTED BEFORE 1962 AND WHOSE PARENTS WERE BORN IN TOWN X" method. This title is self explanatory. Such methods appear arbitrary and lacking a rational basis. They represent the efforts of those closest to the rule-making process to influence the distribution in their favor. Some elements of these methods are probably inevitable under any practical scheme. Within limits, they are of no consequence for an efficiency objective. If carried to extremes however, such methods could seriously diminish the potential economic gains acheivable through allocation methods.

PROPERTIES OF ALLOCATION METHODS

The properties which I wish to discuss are initial distribution, tenure, revocability, transferrability, flexibility and compensatory mechanisms.

The first of these, initial distribution, has been discussed already as part of the description of methods and needs no further discussion.

Tenure

Under ownership, tenure is, by definition, perpetual. Under leasing methods, however, the terms of the lease include such matters as duration and the renewal process which collectively represent tenure conditions. They may also include explicit provisions such as those below. The duration of a lease is extremely critical for aquaculture since a lessee must schedule investment decisions for durable assets. If the lease duration is too short, it may render culture unprofitable. At a less extreme level, too short a lease life may cause investments in technologies and culture techniques which are suboptimal but which have a shorter payback period. A closely related matter is renewal provisions. Reinvestment decisions must be made periodically. If a lessee is in the seventh year of a ten year lease and cannot get a confirmation (or denial) of intent to renew, then that lessee faces intolerable uncertainty for long term investments. A reasonable lease life would probably be at least one and perhaps two or three production/life cycles of the species. With respect to renewal, an expedient policy might be automatic annual renewal unless notified to the contrary. Under such a policy, a lessee always has at least one lease life remaining in which to schedule disinvestment or reinvestment decisions.

Revocability

The issue of revocability may be stated as follows: Is there any conduct by a lessee (owner) which would be sufficient cause for revoking the right to continue culture? At one extreme of the spectrum one can imagine the rights of an owner or a lessee as irrevocable. More probable is a conditional right which can be revoked permanently or suspended temporarily. Possible activities which might trigger such actions would be violation of public health laws or fear of epizootics. Revocability is a further qualification to the tenure conditions described above.

Transferrability

For most commodities in consumer oriented or market economies, transfer via sale or lease is normal. Similarly, use rights whether ownership or lease rights, are usually transferrable to others via resale or release. Such transfers may be subject to restrictions. For example, sub-letting a lease might require notification and a check of records to ensure that the new user has not had a prior revocation of rights as described above.

The advantage to society of transferrability is that it facilitates lease aquisition by the more efficient with compensation of the less efficient seller. A consequence of transferrability is the enrichment of the seller. To some, this may seem like a potential for unjust enrichment. In defense of this consequence, it should be noted that all have benefitted; especially consumers who receive greater supplies at lower cost. Moreover, the windfall gains and losses imposed by public policy changes are ubiquitous; those associated with aquaculture are miniscule by comparison with trade restrictions or changes in national defense policy.

Compensatory Payments

At several points in this paper, reference has been made to "efficiency" versus "distributional" aspects of allocation. The distinction is useful for analysis. However, it is usually the case in practice that gains in efficiency, that is to say, increases in the size of the economic pie, cannot be attained unless adequate provision is made for compensation of individuals who lose when efficiency is increased. From the earlier discussion, it is possible that the incidence of epizootics might be diminished if stocking density could be reduced or if a rotation could be followed as in agricultural crop rotations. Such policies could increase the aggregate economic pie. The individuals asked to forego production would lose, however. A compensatory mechanism for such cases might be a self imposed tax on all culturists in a given estuary, with the proceeds used to compensate those growers who forego production. Another type might be reduced lease fees to individuals who donate seed stock for restocking programs.

ECONOMIC DEVELOPMENT

If fisheries or aquaculture are compared with other sectors of the national economy, it will be found that fisheries and aquaculture are relatively small for most developed nations and likely to remain so. Among the reasons for interest in these sectors is the locations where they take place. Often they are in regions somewhat isolated from major employment opportunities and associated with high regional unemployment. In the capture fisheries, the potential for further employment is largely a negative sum game. More people can be employed by injecting subsidies for vessel construction etc., but the additional yield obtained is small or possibly negative. In mariculture, there are some significant differences which suggest a more promising role in regional economic development.

The first, and perhaps most fundamental one is the existence of property rights for mariculturists. The creation and elaboration of property rights of mariculturists differs greatly between countries but much progress has occurred in the past decade. This process of institutional evolution offers the potential of linking mariculture with a major driving force for economic development; the force of technological progress.

There have been several studies documenting the role of technological progress in economic development and in deferring Malthusian scarcity of natural resources. As applied to mariculture this could include better varieties or strains of organisms, new products or delivery systems. For this progress to occur, it is important to continue exchanges of scientific personnel and information. It is important also to maintain a broad perspective on the problem. I am periodically amazed at the achievements of food scientists in finding new ways to market previously unutilized seafood. In general, the importance of technological progress is in disturbing the status quo and providing entrepreneurs with new, more productive opportunities. It is probably important also to think of mechanisms for dessemination of research knowledge. Programs for technical training or a marine extension program are possibilities. One should also consider the multiple audiences or decisionmakers to be reached and the differing interests of each. For example, the discussion above may not be of great interest

directly to local government officials. Information which may be of greater interest to them are the economic impacts and the income and employment multipliers associated with expansions in the seafood sector. These can be measured using the Input-Output models associated with Professor W. Leontieff. In this connection, I found the modelling discussions of yesterday quite interesting in that the linear compartmental model is isomorphic with the Leontieff model.

CONCLUSIONS AND RECOMMENDATIONS – CONCLUSIONS ET RECOMMANDATIONS

CONCLUSIONS AND RECOMMENDATIONS

1) NATIONAL REVIEWS

National reviews of bivalve culture in member countries and information on the situation in other countries demonstrate that this industry can be of considerable economic and social significance. In countries where it is developed, it represents in terms of economic wealth, employment and supply of sea food, an appreciable part of the fishing industry. This results from some specific advantages that bivalves offer for the cultivation of littoral areas.

In most countries the biological potential for expansion through intensive seeding and ecosystem manipulation, extension of sites or diversification of species is large. This statement applies to both developed and developing countries.

However, considerable differences exist between countries in the development of their industry. This situation reflects the existence of various kinds of opportunities and constraints - e.g. lack of demand or of skill, effects of overstocking in certain areas, diseases, red tides and quality of coastal environment, leasing schemes for sites and conflicts of uses of coastal environment, etc....As a consequence actions to be taken in individual countries will differ and should take into account the stage of development of their industry.

The situation appears particularly favourable for international cooperation. Comparison of national situations should facilitate greatly the identification of constraints as well as the formulation of sound development and management strategies. The steps through which countries with long established industries have developed this activity, the problems they are facing today and the initiatives they are taking to overcome them will be invaluable for countries whose industries are at an earlier stage of development.

The group also noted that large potentials for development also exist in developing countries and that the specific features of bivalve culture will make it particularly suitable to the economic and social conditions prevailling in tropical areas. This is supported by the current development of bivalve culture in Far East countries.

With this situation in mind and the opportunities it offers, the Group listed :

1.1. - the actions which should be initiated without delay, in the field of scientific research and technology, to stimulate and protect shellfish cultivation in member countries,

1.2. - the activities where sharing of national experience and competence appears particularly susceptible to promote the growth of that industry.

2. PATHOLOGY

2.1. - Further development of laboratory methods for diagnosis and research on infections diseases of shellfish is essential.

2.2. - More attention should be paid in characterizing pathologies caused by adverse nutrition and toxic sustances.

2.3. - Increased effort should be made towards development of shellfish tissue cultures with the first step being the formation of an international working group to review the available information and to formulate a collaborative research programme.

2.4. - Steps should be taken to develop meaningful healt certification procedures for shellfish.

2.5. - Studies on the immune response of shellfish should be directed towards host reaction to pathogenic organisms and an assessment made of the feasibility of vaccination to protect cultivated species against disease.

2.6. - Efforts should be made to improve the education of shellfish cultivators in the importance of disease prevention and control.

3. GENETICS

To place the recommendations in the context of the genetic section we emphasize : (1) no single genetic technique can cover the total diversity of problems in managing and improving stocks, (2) that research and development of genetic techniques must be made in concert with other disciplines.

Certainly not all but some shellfish culture systems are amenable to genetic improvement. These should be indentified and developed.

For now, the following specific recommendations are made :

3.1. - listing and classification of national hatchery strains with their characteristics

3.2. - genetic analyses of performance characteristics such as metabolic activities and disease resistance under in situ situations.

4. TECHNOLOGY AND BIOTECHNY

4.1. - hatcheries

The group recommends that hatcheries capability be maintained by countries with shellfish cultivation to continue research in genetics and development of disease resistant stocks of indigenous and introduced species of molluscs. Member countries need to map short and long range strategies to best fit their local situation and objectives. This process can be greatly facilitated through exchange of information between qualified people. Each country will be expected to identify any number of specialists selected according to their expertise with particular species. These persons would be made available by their respective countries for consultation and on-site councelling on any aspect of hatchery, planning, construction, operation and problem solving, including cost reduction. The U.K. and or the U.S.A. could take the lead in the implementation of this recommendation.

4.2. - Nursery and grow- out

The nursery and grow-out systems are major links in the production of commercial molluscs. Member countries have been involved with varying degrees of advancing these systems, with some countries being more advanced than others. However, it shall be noted that information of up-to-date nursery and grow-out techniques are scattered in the litterature and at times incomplete. There needs to be an inventory with descriptions of available techniques, with an analysis of the advantages, disadvantages and cost of each technique for circulation to member countries involved with molluscan culture. This can be accomplished by an exchange of information between qualified people with expertise in nursery and grow-out systems. Each country will be expected to identify any number of specialists in this field. These persons would be made available by their respective countries for consultation and on-site councelling on any aspect of nursery and grow-out construction, operations, and problem solving. France, Japan and Canada could take the lead in the implementation of this recommendation.

5. MANAGEMENT OF SHELLFISH CULTURE ECOSYSTEMS

General :

5.1. - Production of guides characterizing cultured species in terms of their energetic needs for growth, metabolism, reproduction.

5.2. - Suitability of a site for mollusc culture must be established in terms of the following :

past history of fisheries, of aquaculture and disease,

contamination by chemical pollutants, fecal bacteria and naturel toxic biological organisms,

estimates of carrying capacity as obtained through a modelling of pertinent hydrological and biological factors underlying the production of natural food for molluscs.

5.3. - Carry a comparison of knowledge acquired from closed (artificial) and open (natural) systems, in order to improve our understanding of both, to optimize culture operations and to assess the relative merits of aquaculture in closed and open systems.

5.4. - Maintain records on data culture systems, such as biomass in culture growth, mortality, performance, etc.

Regarding the development of aquaculture in specific countries, it is recommended :

5.5. - inventory of appropriate natural sites

5.6. - protection of sites, with the objective of maintaining their natural production protential.

Specifically :

5.7. - It is recommended the formation of an international working group on the modelling of mollusc culture ecosystems.

6 . MANAGEMENT OF EXPLOITATIONS COASTAL AREAS

6.1. Attempts should be made toward comprehensive investigations and efforts should range from basic research to dissemination of research results.

6.2. These efforts, depending on national circumstances may extend, beyond the harvesting sector to food science and marketing

6.3. Member nations should formulate programs suited to their circumstances and, where appropriate, sollicit the exchange of scientific personnel.

6.4. Data research needs for economic and social issues must be defined relative to the problems perceived in each nation. Suggested minimal needs would be weight and values of harvest, both aggregate and per unit area, of cultured species.

6.5. Where there exists overstocking or inter-use conflicts, may be desirable to study the nature of the problem as well as methods of conflict resolution.

CONCLUSIONS ET RECOMMANDATIONS

1 - BILANS NATIONAUX

Les bilans de l'état de la conchyliculture dans les pays membres et les informations sur d'autres pays démontrent que cette industrie peut être d'une importance économique et sociale considérable. Dans les pays où elle est développée, elle représente en terme de richesse économique, d'emplois et dans l'alimentation, un part importante de la pêche. Ces résultats proviennent des avantages qu'offrent la culture des bivalves.

Dans la plupart des pays il existe un grand potentiel biologique et l'expansion peut se faire par un ensemencement intensif et une modification de l'écosystème, par l'extension des sites ou par une diversification des espèces. Ce constat s'applique aux pays ayant une conchyliculture développée ou en voie de développement.

Toutefois, des différences considérables entre pays existent dans les stades de développement de cette activité. Cette situation reflète l'existence de différents types d'opportunités et de contraintes : par exemple l'absence de demande ou de compétence technique, les effets de la surpopulation dans certaines zones, les maladies, les marées rouges, et la qualité de l'environnement littoral, les projets de location et les conflits pour l'usage du littoral, etc.

Cette situation semble particulièrement favorable à une coopération internationale. La comparaison des situations nationales devrait grandement faciliter l'identification des contraintes aussi bien que la formulation de solides stratégies de développement et d'aménagement. Ces activités ont été développées par étapes dans les pays qui ont une longue tradition conchylicole. Les probmèmes auxquels ils ont à faire face aujourd'hui et les initiatives qu'ils sont en train de prendre pour les résoudre seront d'une valeur inestimable pour les pays dont l'industrie en est à un jeune stade de développement.

Le groupe note également que des potentiels existent aussi dans les pays en voie de développement et que le trait spécifique de l'élevage des mollusques le rend particulièrement adapté aux donditions économiques et sociales rencontrées dans les zones tropicales. Ce constat est étagé par le développement courant de l'élevage des mollusques en Extrême-Orient.

Tenant compte du constat de cette situation et des opportunités offertes le groupe retient :

- les actions qui devraient être entreprises rapidement, dans les domaines de la recherche et de la technologie, pour stimuler et protéger l'élevage des mollusques dans les pays membres ;

- Les activités où le regroupement des différentes compétences et expertises nationales semble particulièrement susceptible de promouvoir la croissance de cette industrie.

2 - PATHOLOGIE

2.1. Le développement de méthodes de laboratoire pour le diagnostic et la recherche des maladies de mollusques est essentiel.

2.2. Plus d'attention devrait être accordée à la caractérisation des phénomènes pathologiques d'origine nutritionnelle ou dus à des substances toxiques.

2.3. L'effort devrait être accru pour la culture des tissus de mollusques. Un premier pas pourrait être la formation d'un groupe de travail international dont le but serait de recenser les informations existantes et de proposer un programme de recherche en collaboration.

2.4. Des démarches pourraient être entreprises pour établir une véritable procédure de certification de santé des mollusques.

2.5. Des études sur les mécanismes de défense des mollusques devraient être conduits en s'orientant vers les réactions de l'hôte aux organismes pathogènes. La faisabilité biologique de la vaccination devrait être évaluée.

2.6. Un effort devrait être fait pour informer et éduquer les conchyliculteurs sur l'importance des maladies et des prophylaxies.

3 - GENETIQUE

Pour replacer les recommandations dans le contexte du groupe génétique, nous soulignons : 1) aucune technique génétique ne peut couvrir l'ensemble des problèmes de gestion et d'amélioration des stocks, 2) la recherche et le développement des techniques génétiques doivent être effectués conjointement à d'autres disciplines ; 3) seules quelques espèces sont susceptibles, à ce jour, d'être utilisées pour l'amélioration génétique. Celles-ci devraient être identifiées et utilisées.

3.1. Un inventaire et une classification des souches en écloseries, en mentionnant leurs caractéristiques.

3.2. Des analyses génétiques des critères de performance tel que l'activité métabolique et la résistance aux maladies dans le milieu naturel.

4 - TECHNOLOGIE ET BIOTECHNIE

4.1. Ecloseries

Le groupe recommande que les écloseries de mollusques soient maintenues dans les pays pour poursuivre les recherches en génétique et sur les populations indigènes ou non résistantes aux maladies. Les pays membres ont besoin de batir des stratégies à court et long terme pour s'accorder convenablement avec les objectifs et les situations locales.

Ce travail peut être facilité par l'échange d'informations entre les spécialistes. Chaque pays devrait identifier des spécialistes pour différentes espèces. Ces personnes devraient être mises à disposition par leurs pays pour la consultation sur le choix des sites et sur les différents aspects de l'écloserie : les plans, la construction et la résolution des problèmes incluant la réduction des coûts. La Grande-Bretagne ou les Etats-Unis pourraient être leader pour les mises en oeuvre de cette recommandation.

4.2. Nourricerie et grossissement

Les techniques de nourricerie et d'élevage sont étroitement associées à la production des mollusques. Les pays membres travaillent plus ou moins sur ces techniques, certains pays étant en avance sur d'autres. Cependant, il peut être noté que les informations dans la littérature sont incomplètes et dispersées. Le besoin d'un inventaire comprenant le descriptif des techniques disponibles, l'analyse des avantages et des inconvénients et des coûts de chaque technique devrait être réalisé pour communication entre les différents pays intéressés. Ceci peut être réalisé par un échange des informations entre experts . Chaque pays devrait identifier des spécialistes de ces domaines. Ces personnes pourraient être mises à disposition par leur pays pour consultation sur le choix des sites et sur les différents aspects de la construction des nurseries et la résolution des problèmes. La France, le Japon et le Canada pourraient être leader pour la mise en oeuvre de cette recommandation.

5 - EXPLOITATION DES BIOTOPES CONCHYLICOLES

Généralités

5.1. Production d'un mémoire caractérisant les espèces cultivées par des données sur leur besoins énergétiques pour la croissance, le métabolisme et la reproduction.

5.2. Définir l'aptitude d'un site pour la culture des mollusques d'après les termes suivants :
- histoire des pêches, de l'aquaculture et des maladies,
- contamination par des polluants chimiques, par des bactéries et par des organismes toxiques,
- estimation de la capacité trophique obtenu par une modélisation des facteurs hydrologiques et biologiques fondamentaux pour la production naturelle de nourriture.

5.3. Comparer les connaissances acquises dans les systèmes fermés et ouverts, dans le but d'améliorer nos connaissances, de rentabiliser les cultures et d'évaluer les avantages de l'aquaculture suivant le système.

5.4. Soutenir l'enregistrement des données de culture, telles la biomasse, la croissance, la mortalité, les performances,etc.

Développement spécifique de l'aquaculture, dans certains pays nous recommandons :

5.5. L'inventaire des sites naturels appropriés.

5.6. La protection des sites en vue de maintenir leur potentiel de production naturelle.

Particulièrement :

5.7. Nous recommandons la formation d'un groupe de travail international sur la modélisation des écosystèmes conchylicoles.

6 - GESTION DE L'EXPLOITATION DES ZONES COTIERES

6.1. Des efforts devraient être fait avec les données existantes en les classant depuis les recherches de fondamentales jusqu'à la divulgation des résultats.

6.2. Ces efforts dépendant des circonstances nationales peuvent être étendus à la tranformation et à la commercialisation des produits.

6.3. Les pays membres, en fonction des circonstances et quand cela est nécessaire, pourraient établir des programmes et solliciter des échanges de personnels.

6.4. Les besoins de données scientifiques pour les questions économiques et sociales doivent être définis en fonction des problèmes perçus dans chaque pays. Les besoins minimum suggérés devraient être le poids et la valeur des récoltes, totale et par zone, des espèces cultivées.

6.5. Dans les secteurs à surpopulation ou à conflits d'utilisation, il paraît utile d'étudier la nature des problèmes aussi bien que les méthodes pour résoudre les conflits.

APPENDIX

LIST OF PARTICIPANTS

CANADA

Dr Pierre BELAND
Fisheries Ecology Research Center
310, avenue des Ursulines
RIMOUSKI
Québec G5L 3A1

Dr René LAVOIE
Fisheries Research Branch
Departement of Fisheries and Oceans
P.O. Box 550
HALIFAX, N.S. B3J 257
Canada

Dr André MALLET
Marine Ecology Laboratory
Bedford Institute
DARTMOUTH, B2Y 4A2
Nova Scotia

GERMANY

Dr Mathias SEAMAN
Institut für Meereskunde
Düstermbrooker Weg 20
2300 KIEL
Allemagne Fédérale

ITALY

Dr Paolo BREBER
INSTITUTO C.N.R.
Via Fraccacreta 1
71010 LESINA (FG)
Italie

Dr Italo Dante DE MURTAS
ENEA
Fare Bioag
C.P. 2400
00100 ROMA
Italie

Pr A. RENZONI
Dippartimento Biologia
Ambientale
University of Siena
Via delle Cerchia 3
53100 SIENA
Italie

JAPAN

Dr Hisashi KAN-NO
Tokai Regional Fisheries
Research Laboratory
5-5-1- Kachidoki, Chuo-Ku
TOKYO 104
Japon

UNITED KINGDOM

Dr Barry J. HILL
Fish Diseases Laboratory
M.A.F.F.
WEYMOUTH DORSET DT 1 8UB
Grande-Bretagne

Dr C. E. PURDOM
M. A. F. F.
Fisheries Laboratory
LOWESTOFT SUFFOLK
Grande-Bretagne

UNITED STATES OF AMERICA

Dr Kenneth K. CHEW
Division of Aquaculture and
Invetebrate Fisheries
School of Fisheries
SEATTLE, WASHINGTON 98.195
Etats Unis

Pr John M. GATES
Department of Resources Economics
Lippitt Hall
University of Rhode Island
KINGSTON, RI 02881 - 0814
Etats-Unis

Pr Louis LEIBOVITZ
Marine Biological Laboratory
Lab. For Marine Animal Health
WOODS HOLE, MASSACHUSSETTS 02543
Etats-Unis

Dr Arlene LONGWELL
National Marine Fisheries
NOAA US DEPT. COMMERCE
Milford Laboratory
212 Rogers avenue
MILLFORT CT 06460
Etats-Unis

FRANCE

M. Michel AUFFRET
Laboratoire de Pathologie
Faculté de Médecine
B.P. 815
29279 BREST CEDEX

M. Cédric BACHER
IFREMER
Mus de Loup
B.P. 133
17390 LA TREMBLADE

M. Louis-Pierre BALAY
DPMCM
Secrétariat d'Etat
chargé de la mer
3 place de Fontenoy
75700 PARIS

M. Jean-Paul BERTHOME
IFREMER
rue de l'Ile d'Yeu
B.P. 1049
44037 NANTES CEDEX

Mme Françoise BLANC
Laboratoire de Zoogéographie
Université Paul Valéry
B.P. 5043
34032 MONTPELLIER CEDEX

M. Alain BODOY
IFREMER La Tremblade
Mus de Loup
B.P. 133
17390 LA TREMBLADE

M. Jean Robert BONAMI
U. S. T. L. ERPAM
av. Eugène Bataillon
34060 MONTPELLIER CEDEX

M. Marc BONNET
IFREMER
66 avenue d'Iéna
75116 PARIS

M. Bernard CHEVASSUS AU LOUIS
INRA Dépt. d'Hydrobiologie
78350 JOUY-EN-JOSAS

M. Michel COMPS
IFREMER
1 rue Jean Vilar
34200 SETE

Mme Marie-José DARDIGNAC
IFREMER
74 allée du Mail
17000 LA ROCHELLE

M. Jean-Pierre DELTREIL
IFREMER
63 boulevard Deganne
33130 ARCACHON

M. Jean Louis DENOYELLE
Délégation Régionale
à l'Aquaculture
14, rue Villeneuve
17000 LA ROCHELLE

M. Jean Marc DESLOUS-PAOLI
IFREMER
Mus de Loup
17390 LA TREMBLADE

M. Jean Paul DRENO
IFREMER
rue de l'Ile d'Yeu
B.P. 1049
44037 NANTES CEDEX

M. Claude FAIVRE
ADACO
14 rue Villeneuve
17000 LA ROCHELLE

M. Jean- Pierre FLASSCH
IFREMER
B.P. 337
29273 BREST CEDEX

M. Philippe GOULETQUER
IFREMER
Mus de Loup
17390 LA TREMBLADE

M. Paul GRAS
IFREMER
Mus de Loup
B.P. 133
17390 LA TREMBLADE

M. Henri GRIZEL
IFREMER
12 rue des Résistants
56470 LA TRINITE-SUR-MER

M. Maurice HERAL
IFREMER
Mus de Loup
B.P. 133
17390 LA TREMBLADE

M. Edouard HIS
IFREMER
63 boulevard Deganne
33120 ARCACHON

M. Jacques LEBRETON
Laboratoire de Zoologie
CNRS 679
Université de Caen
14032 CAEN CEDEX

M. Albert LUCAS
Université de Bretagne Occidentale
Laboratoire de Zoologie
Faculté des Sciences
29287 BREST CEDEX

M. Serge MAESTRINI
CREMA L'Houmeau
Case 5
17137 NIEUL-SUR-MER

M. Henri MASSE
Centre d'Océanographie de Marseille
Station Marine d'Endoume
13007 MARSEILLE

Melle Danièle MAURER
IFREMER
63 boulevard Deganne
33120 ARCACHON

M. Eric MEURIOT
IFREMER
B.P. 1049
44037 NANTES CEDEX

M. Eric MIALHE
IFREMER
12 rue des Résistants
56470 LA TRINITE-SUR-MER

M. Alain MICHEL
IFREMER
66 Avenue d'Iéna
75116 PARIS

M. Alain PARACHE
Station Marine d'Endoume
rue de la Batterie des Lions
13007 MARSEILLE

M. Robert POGGI
IFREMER
rue de l'Ile d'Yeu
B.P. 1049
44037 NANTES CEDEX

M. Gilles PORTERES
Laboratoire de Biologie et
Biochimie Marines
I.U.T.
rue de Roux
17026 LA ROCHELLE CEDEX

Melle Edwige QUILLET
IFREMER
B.P. 337
29273 BREST CEDEX

M. Alain RIVA
Fondation Océanographique RICARD
Ile des Embiez - Le Brusc
83140 SIX-FOURS-LES-PLAGES

M. Jean TARDY
Laboratoire de Biologie et
Biochimie Marines
I.U.T. - rue de Roux
17026 LA ROCHELLE CEDEX

M. Jean Paul TROADEC
IFREMER
66 avenue d'Iéna
75116 PARIS

M. Christian VIVAGES
Laboratoire de Pathologie comparée
USTL
Place Eugène Bataillon
34060 MONTPELLIER CEDEX

M. Jacques WEBER
IFREMER
B.P. 1049
44037 NANTES CEDEX

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